Beware your neighbours: interactions shape population dynamics in natural grassland communities

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Submitted in fulfillement of the requirements for the degree of Master of Science

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Dedicated to my family and friends for their loving support.

Contents

Abstract 9

Introduction 11

The importance and variability of interactions between species 11
Estimating interaction strengths 12
A framework for modeling population dynamics 14
A Bayesian approach to modeling 14
Aims and hypotheses 15

Quantifying the impact of interactions in New Zealand grassland communities 17

Abstract 17
Introduction 17
Methods 19
Results 28
Discussion 38

How plant interactions vary by guild and along two abiotic gradients 43

Abstract 43
Introduction 43
Methods 46
Results 54
Discussion 62

Synthesis 69

Species interactions 69

Environmental effects on species interactions 70

Implications for theory and applications 71

Future directions 73

Conclusion 76

Bibliography 77

Acknowledgments 91

Preface

This thesis has been written as two stand-alone scientific articles. Both articles, *"Quantifying the impact of interactions in New Zealand grassland communities"*, and *"How plant interactions vary by guild and along two abiotic gradients"*, are intended to be submitted for publication. These articles build upon the same initial model framework, and hence share some similarities in the Methods, though I have attempted to minimise this. Preceding these articles is a wider review of the relevant literature than that presented in the introductions of the articles themselves. Finally, in *"Synthesis"*, I discuss the relevance of the two articles to each other, the existing scientific literature, and their application in ecology.

Abstract

Interactions between species have long been recognised as being of major importance to patterns of diversity and abundance, yet our knowledge of how interactions operate and vary in natural plant communities remains incomplete. In such diverse system, interactions are both numerous and highly variable, and they depend on both abiotic and biotic context. This makes quantifying interaction strengths between species in natural communities a difficult and complex task, but it is also a necessary one if we are to uncover the driving forces underpinning this variation.

Species interactions are an important component of grassland population dynamics, where plants compete for sunlight, space, nutrients and water. Furthermore, the short generation times of most grassland plant species makes them a useful system for examining the effects of interactions. The National Vegetation Survey databank, operated by Landcare Research, hosts time-series of grassland plant abundances from several hundred plots and collected over the span of several decades. I proposed to exploit the potential of this data set in order to examine the effects of interactions on plant population dynamics.

My first hypothesis was that including species interactions in models of population dynamics would improve our ability to predict changes in plant abundance in natural grassland communities. To test this hypothesis, I compared the fits of a series of models which included interactions in increasingly complex and biologically meaningful ways. I found that including interactions improved predictions for the overwhelming majority of species. The most successful model included every pairwise interaction, which allowed us to estimate measures of interaction strengths between species. In turn, the distribution of these interaction strengths provided insights into potential community-level differences in stability. The results prsented here suggest these differences were driven by elevation, which weakened interactions, and the presence of exotic species, who tended to have

stronger interactions than native species.

My second study investigated how interactions between species varied along multiple abiotic gradients. I estimated interaction strengths between focal species and four guilds of competitors — forbs, graminoids, woody species and non-woody others — occurring over a range of elevations and latitudes. Both gradients had varying effects on the mean interaction strengths of each competitor guild. On average, increasing elevation and latitude made interactions with forbs facilitative, whereas interactions with graminoids and woody species became less facilitative and more competitive. This variation in interaction effects might be a reflection of the different optima conditions for each group of species.

Together, the work that makes up this thesis suggests that interactions between species can be regarded as an important driver of changes in plant abundance in these grassland communities. Plant-plant interactions should be included in models of population dynamics in order to improve predictions of changes in abundance. Furthermore, including interactions also uncovers how variable their effects are, to both environmental conditions and identity of the interaction partner. In particular, the relationships between elevation, species functional guild and biological status affected species interactions in complex, and at times unexpected ways. This has important implications for our understanding of how plant interactions shape grassland community dynamics, and thereby how these communities might respond to biotic and abiotic threats.

Introduction

Interactions between species are as variable as species themselves. They are dynamic over time and space, and vary with the identity and abundances of the interacting partners. This variability between interactions can complicate their study, especially in natural communities where they might be affected by any number of abiotic or biotic factors. However, interactions have a strong impact on community patterns of abundance and distribution, and hence on community structure and stability. It is therefore exceedingly valuable to find tractable ways to quantify interactions strengths in natural communities and explore the nature of this variation.

The importance and variability of interactions between species

Because interactions can affect the abundance and distribution of species, they have an impact on the overall structure and composition of communities (Gurevitch et al., 1992; Harpole and Tilman, 2006; Chu and Adler, 2015). They can drive speciation (Svanbäck et al., 2007; Lankau, 2012) and coexistence (Bengtsson et al., 1994), affect ecosystem functioning (Michalet et al., 2006; Yachi and Loreau, 2007) and alter a community's susceptibility to disturbances and extinction (Bascompte et al., 2005; Fowler, 2010, 2013). Ultimately, the pattern of interactions in a community is intimately coupled to its stability and diversity (May, 1972; McCann et al., 1998; Ives et al., 2003; Neutel et al., 2002; Tang et al., 2014). Measuring interactions and understanding how they can vary can help us explore these community-level effects.

One major complication in the study of species interactions is how much they can change (Poisot et al., 2015). Thompson (1988) was one of the first to review how interactions varied in their outcomes, both within populations and across environmental gradients. Under different conditions such as high or low soil moisture for example, an interaction between two same species at the same abundances can switch from being positive to negative (Bertness and Callaway,

1994; Callaway, 1995; Pugnaire and Luque, 2001; He et al., 2013; Mod et al., 2016). An interaction between two species can also be mediated by the presence of a third species, for example if that third species modifies micro-environmental conditions or traits of the focal species (Wootton, 2002; Werner and Peacor, 2003). Knowing the outcome of an interaction in one situation does not necessarily allow us to predict the same outcome under different conditions (Thompson, 1988; Chamberlain et al., 2014). We must thus keep in mind that interactions are dynamic and context dependant.

When one thinks of an interaction driving the abundances of respective species, a typical example would be a predator and prey cycling through high and low abundances (Elton, 1927). However, any two species can affect the abundance of each other without resorting to direct consumption, for example by competing for a shared resource. This type of interaction is crucial to plant communities, which will form the focus of this thesis. Plants compete for space, sunlight and nutrients, sometimes to the detriment of other individuals (Went, 1973; Grace and Tilman, 1990). They can also promote the growth of other species, for example by fixing nitrogen in the soil (Temperton et al., 2007; Brooker et al., 2008). Hence within a plant community, interactions can have significant effects on patterns of distribution, diversity and abundance (Connell, 1983; Goldberg and Barton, 1992; Bengtsson et al., 1994). In fact, a substantial amount of research on interactions and their effects has focused on plant-plant interactions.

Estimating interaction strengths

Initially, interactions were simply described, for example as mutualistic (+/+), parasitic (+/-) or commensal (+/0), but this qualitative categorisation was not sufficient to capture the full range of interaction effects (Thompson, 1988). Instead, ecologists switched to the concept of interaction strength in an attempt to directly quantify the effect on one species on another (Wootton and Emmerson, 2005). This approach seems intuitive, though a variety of definitions and estimation methods have been proposed, in part due to the context dependency described above (see Berlow et al., 2004, for a particularly comprehensive review of theoretical and empirical definitions of interaction strength). In this thesis, I use the definition provided by Laska and Wootton (1998): interaction strength is the per capita effect of one species on another, within a given (typically short) unit of time. Importantly, this particular concept of interaction strength does not require any assumptions about the equilibrium state of the com-

munity and provides the basis from which most other measures of interaction strength are derived (Laska and Wootton, 1998; Wootton and Emmerson, 2005).

Interaction strengths described in the manner above can be estimated as coefficients in multi-species models of population dynamics (Laska and Wootton, 1998; Kokkoris et al., 2002; Ives et al., 2003; Berlow et al., 2004). In these models, variation in the abundance of a single, focal species is driven by population growth, which is itself affected by the abundance of interacting species. Fitting these models as multivariate regressions to time-series data allows us to get estimates of the pairwise interaction strengths between the focal species and each of it's interaction partners (Ives et al., 2003; Adler et al., 2007; Pantel et al., 2014).

This method requires long-term data on the abundances of all species of interest. Often, such data can be made available from experimental plots, where competing species are grown together at varying densities to measure the effect of one on another (Law and Watkinson, 1987; Freckleton et al., 2009) . Using such experimentally assembled data, however, limits the number of interacting species and also means that the full breadth of processes acting within natural communities is not necessarily captured. Due to the context dependency of interactions, this presents difficulties when attempting to infer the outcomes or importance of interactions in natural communities.

On the other hand, fitting interaction strengths to observed data from natural communities presents it's own set of difficulties. Such communities are typically diverse, and can hence require a large number of parameters if the goal is to estimate every pairwise interaction. One common alternative is to average the effect of interactions, either across similar species (e.g. by guild) or across the whole community (Levine and HilleRisLambers, 2009; Godoy and Levine, 2014) . Attempts to capture the full complexity of interactions and their context dependency in natural communities have been made (Kunstler et al., 2012), but remain rare (Freckleton et al., 2009) and often require advanced statistical and computing methods. In addition, a model framework capable of capturing the relevant variation and incorporate interactions must be established. This task was an essential feature of both studies presented in this thesis.

A framework for modeling population dynamics

The Theory of Island Biogeography (TIB), initially developped by Mac Arthur and Wilson (1967), models the number of species on an island as the result of colonisation and extinction processes. Both processes are affected by current species diversity, and the theory treats species as functionally equivalent. Extinction is stochastic and decreases with island size, whereas the colonisation rate by new species increases as an island becomes closer to the mainland (the source of new species).

During the same time, Levins (1970) explored the dynamics of a set of local populations occupying many interlinked patches — a metapopulation. In theory, a patch can refer to any spatially discrete habitat – lake, meadow, island, patch of soil. Instead of modelling the flux of species as in the TIB, Levins' framework focuses on the flux of populations between these spatially discrete habitats, which can also become saturated by too many individuals. Each patch is given a probability of extinction and colonisation depending on whether it is occupied or empty, with the colonisation probability typically driven by a species' dispersal ability, distance between patches, and the proportion of patches already occupied.

Both theories are widely generalisable and have been successfully used to model the dynamics of diverse systems which at first glance share little with the original inspiration. Given that both approaches explicitly deal with colonisation and extinction rates, they can be combined in a relatively straightforward manner. Such a model dealing with a system of linked patches can allow colonisation of new patches to occur from both immigration between patches (the Levins model) and immigration from an outside source (the mainland in the TIB). Furthermore, both initial models (and any hybrid) are flexible and can be further modified to include the effects of abiotic and biotic factors, such as species interactions.

A Bayesian approach to modeling

Bayesian approaches to data analysis are increasingly being used in ecology (Clark, 2005; Cressie et al., 2009; Hobbs, 2009; Hooten and Hobbs, 2015) and have been argued to allow for stronger conclusions to be drawn from large-scale experiments with fewer replicates (Ellison, 1996). Bayesian methods have been popular in population and community ecology (for example Ellison, 2004) including predator-prey interactions, but less so for estimating competitive interaction

strengths.

Using a Bayesian framework provides several clear benefits. Firstly, parameter inferences are valid regardless of sample size (Dorazio, 2016), which is particularly useful when they are few observations, or the data is heavily zero-inflated (as is commonly the case in ecological datasets). Secondly, Bayesian models tend to be highly accomodating of complexity (Clark, 2005). Last but not least, any and all Bayesian models can be fitted to the data using Monte Carlo Markov Chain algorithms, even when the parameters cannot be estimated numerically using traditional frequentist methods (Dorazio, 2016).

Underpinning methodological differences between Bayesian and frequentist statistics lies a philosophical difference in statistical inference. A full analysis of these differences is beyond the scope of this thesis, but one important distinction for the research to follow comes in their treatment of model parameters. Unlike frequentist inference, which treats model parameters as fixed values reflecting a 'true' quantity, Bayesian inference considers those parameters to be random variables (Ellison, 1996, 2004). Hence when estimating values of interaction strength in the following chapters, I am not arguing that they are representative of a fixed, biological reality. Rather they are extrapolated from the data and reflect underlying complex patterns and relationships. The resulting models are therefore not mechanistic in nature and hence stand in contrast to approaches such as R* theory (Tilman, 1982). Moreover, though the concept of parsimony is applied, it is not the stated goal of our approach. Instead, I aim to improve our predictions of the observed variation in plant abundances. Despite the lack of an explicit mechanism, such predictive ecology remains highly valuable (Evans et al., 2013) and can help assess the distance between current theory and practice.

Aims and hypotheses

The overarching aim of this thesis is to explore how incorporating interactions between species can improve our preditions of plant population dynamics in natural, diverse communities. In both studies, I develop and parameterise a series of candidate models with time-series data of New Zealand grassland abundances and compare them on the basis of predictive ability. I adopt a Bayesian framework which allows us to incorporate prior knowledge of parameter estimates and resolve highly parameterised models.

Estimating every pairwise interaction within a diverse community is a demanding task but can shed light on the community's structure and stability. In our first study, I examine whether such an endeavour is analytically feasible and compare it to simpler alternatives which treat the effect of interactions as an average, community-wide effect. I hypothesise that for a majority of species, including interaction strengths which vary according to neighbour identity will improve model predictions.

We are aware of the context-dependency of interactions but few studies evaluate this variability along multiple abiotic gradients in natural communities. In my second study, I therefore explore if and how estimates of interaction strength vary along both elevation and latitude. I hypothesise that models include the effects of both interactions and abiotic gradients will receive the most support. Then, I observe how interaction strengths between guilds of species are differentially affected by environmental variation and draw inferences from our estimates of interaction strength.

Together, these two studies investigate how interactions can affect model predictions and vary with species identity and abiotic factors. These results help identify gaps between theory and empirical applications of population models in an effort to better predict community dynamics in diverse communities. They also lead to a deeper understanding of how interaction outcomes may vary between communities and across landscapes.

Quantifying the impact of interactions in New Zealand grassland communities

Abstract

Both positive (facilitation) and negative (competition) interactions impact plant abundances and shape patterns of community composition and abundance. Few studies, however, have explicitly quantified these relationships in diverse natural assemblages due to large data and computing requirements. I use a time series of New Zealand grassland communities to parameterise models which explore the impact of species interactions and how they relate to other processes affecting population dynamics, such as dispersal or recruitment. I considered models that generalise interaction strength over species, as well as formulations which allow for specificity of interactions. Despite penalising candidate models for increased complexity, I find that making interactions species-specific— that is, adding a term for every pairwise interaction — gives the greatest improvement to model predictions. Models that did not include interactions were overwhelmingly rejected. Though the majority of interactions are weak to non-significant in the best-supported model, I observe significant differences in the range of interaction strength experienced by species at different sites. This supports the concept that the strength of interactions between species is context-dependent.

Introduction

Plants compete for space, sunlight and nutrients. Their interactions drive decreases and increases in the abundances of other species in the community, with the increased abundance of one species generally detrimental to other species in the system (Grace and Tilman, 1990). Not all interactions, however, are negative. Some interactions facilitate neighbours, for example by attracting pollinators or buffering environmental conditions (Brooker et al., 2008; Thomson, 1981; Went, 1942). Not all interactions are between different species either.

Individuals of the same species also interact with each other, still in competition for space, sunlight and nutrients (Grace and Tilman, 1990). These intraspecific interactions can act to moderate the effects of interspecific competition, without which competitively dominant species eventually exclude other species from a community. Together, intraspecific and interspecific interactions are thus widely theorised to be of fundamental importance to community diversity, composition and abundance patterns (Gurevitch et al., 1992; Harpole and Tilman, 2006). Despite this appreciation for the contribution of interactions to species coexistence, few studies have quantified them in natural communities (Chu and Adler, 2015).

Though species living in natural communities almost always interact with more than one species at any one time and place, studying pairwise interactions between species is a useful experimental approach for understanding species coexistence (Levine and HilleRis-Lambers, 2009; Godoy and Levine, 2014; Kraft et al., 2015). The interaction strength between two species, typically denoted α, represents the magnitude of the effect of one species on another and captures the results of differences in resource use and availability, responses to environmental factors, and other factors which can indirectly affect the outcome of species interactions (Wootton and Emmerson, 2005). Estimating these interaction strengths can allow us to better understand the dynamics of multispecies communities and provides a starting point for investigating niche differences (Adler et al., 2007), ecosystem stability (Tang et al., 2014), extinction cascades (Fowler, 2010, 2013; Nilsson and McCann, 2016) and even community changes in response to climate change (Alexander et al., 2016).

Grasslands are commonly used for studies of plant species interactions and coexistence dynamics in both experimental and observational studies (for example, see Grace and Tilman, 1990; Godoy and Levine, 2014; Chu and Adler, 2015; Kraft et al., 2015; Staples et al., 2016). They are a typically competitive system, where the results of non-trophic interactions are detectable in community-level patterns of abundance and composition. Grasses are generally fast-growing with short generation times, which allows the effects to be measured across multiple generations. Typical experimental approaches grow focal species at varying densities of competitors to measure changes in biomass, abundance, seed production or survival (Freckleton et al., 2009).

Observational data from natural communities can also be used to measure interaction strengths among species (Laska and Wootton,

1998; Adler et al., 2007; Ives et al., 2003). This can be done by applying a dynamic regression analysis to time-series data of species abundances. This approach provides similar estimates of interaction strength to experimental pairwise studies (Pfister, 1995) and benefits from capturing processes which are hard to measure in an experimental setting. The downside of this approach is that it requires the fitting of a large number of parameters (including one for every pairwise interaction) which can be data, computationally and statistically demanding when used to study diverse communities. This approach has thus been largely restricted to the study of small assemblages of less than a dozen species where sufficient data have been collected (for example, Coomes et al., 2002; Adler et al., 2010; Chu and Adler, 2015. As an exception, see Kunstler et al., 2012).

In this study, I attempt to quantify pairwise interaction strengths between 56 to 133 species from three highly diverse, natural grassland communities in New Zealand. To determine how important species interactions are for modelling patterns of abundance and diversity, I ask the following questions:

1. Does the inclusion of species interactions to models of population dynamics improve predictions of future changes in abundance ?
2. Is the inclusion of every pairwise interaction feasible and an improvement over generalising interactions across competitors ?
3. Does model improvement vary depending on whether interactions are included within the colonisation or extinction rate ?

Based on these results, I then analyse the model which shows the highest overall improvement to predictions of species population dynamics. I relate the range and distribution of interaction strengths to differences between the three communities.

Methods

Data

I downloaded plant-abundance time-series from the New Zealand National Vegetation Survey databank (NVS) in September 2015. Of all data available there, I selected permanent grassland transects which had been remeasured twice yearly with the species-frequency surveying method (SFS) detailed in Wiser and Rose (1997). Grasslands provide an appropriate model system because competition has been identified as a prominent assembly process in grasslands world-wide (Harpole and Tilman, 2006), and the short generation

times of many grasses means community changes can be observed over shorter collection times than systems dominated by longer-lived species such as forests. I focused on the subset of NVS grassland datasets which were measured with SFS as it was the most common survey approach in the NVS database and limiting studies to one surveying approach only ensured that included datasets were comparable. The SFS method is a relatively coarse measure of composition, which makes it less sensitive to small-scale changes within study sites (Wiser and Rose, 1997). In this method, a surveyor places 50 steel wire rings (called 'subplots') at regular intervals along a 20 metre transect as shown in Figure 1. All live plants rooted within the ring are then recorded as present. The frequency of a species' along a transect is then given by the number of occupied subplots along the transect.

Figure 1: Measuring a subplot using the 15-cm diameter steel wire ring. Photo taken from Wiser and Rose (1997).

This SFS method determines how often a species is present or absent in a series of subplots. Therefore it is not a direct measure of abundance but rather provides an estimate of the probability $p_{i,t}$ of encountering a species i in each subplot at time t. For example, a species with a transect frequency of 0 is absent from all subplots but not necessarily absent from the community, which translates to a very low but non-zero probability of being encountered. For this study, all measures of transect frequency were transformed into probabilities of being encountered, and I assume that variation in this probability follows from variation in abundance.

In total 38 transects from 3 sites in New Zealand met the sampling requirements for this study. This included 10 transects at Earnscleugh (45 °15′ to 45 °8′ S, 169 °16′ to 169 °18′ E), 5 transects at Galloway (45 °15′ S, 169 °35′ E) and 23 transects at the Mavora site (45 °7′ to 45 °14′ S, 168 °7′ to 168 °11′ E) (Figure 2). All transects at Earnscleugh and Galloway were measured eight times between 1983 and 1986, while all Mavora transects were measured twice in 1986 only. Measures were 5 to 7 months apart. Earnscleugh transects ranged from 240 to 410 meters in elevation whereas Galloway transects were all at 570 meters. Both sites were dominated by exotic forbs and graminoids. In contrast, Mavora is higher with transects ranging from 635 to 800 meters elevation and was mainly composed of native shrubs, forbs and graminoids.

Since uncommon species are unlikely to result in widespread competitive effects, I excluded uncommon species from the dataset by removing those species that were consistently found in fewer than 10% of subplots in a single transect (Adler et al., 2013). This resulted in the removal of 56 species from the dataset and left us with 173

species across all sampling points.

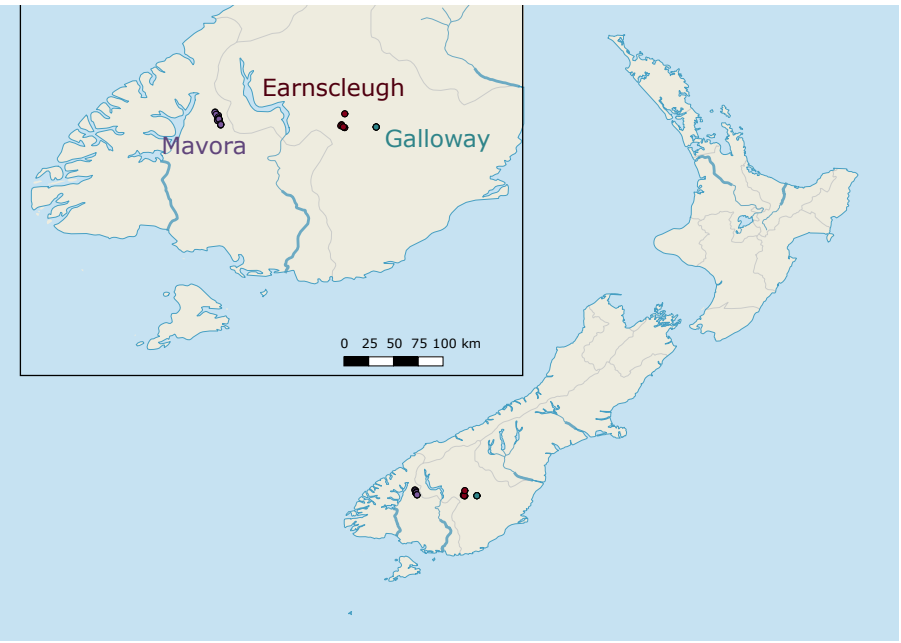

Figure 2: Map of transects and study sites.

Model framework

Given my interest focused on changes in community composition, I built my model framework based on a combination of the Theory of Island Biogeography (TIB) Mac Arthur and Wilson (1967) and Levins' (1970) patch-occupancy model, both of which predict a species' future abundance as the result of colonisation and extinction processes. Both models are simple, well-supported and easily generalisable, and the latter has also been used to successfully model New Zealand grassland dynamics in the past (Russell et al., 2005). Using this framework, I varied if, where and how interactions between species were added to the models according to specific hypotheses on how interactions may affect population dynamics, as detailed below and in the following section.

From observation period to observation period, the simplest possible way to measure variation in the probability of being encountered along a transect is a random walk where the occupancy of species i at time $t+1$ is sampled from occupancy at time t, such that:

$$p_{i,t+1} \sim p_{i,t} \tag{1}$$

This served as my null model, where changes in abundance are driven by stochasticity alone. I compared this null model to seven

more biologically realistic alternative models. My next *no interactions* model is a combination of the TIB and Levins models, which models occupancy probability as the outcome of colonisation and extinction patch-occupancy processes along a transect, given by:

$$p_{i,t+1} = p_{i,t} + c_i(1 - p_{i,t}) - e_i p_{i,t} \tag{2}$$

where c_i is the colonisation rate into unoccupied subplots and e_i is the extinction rate in occupied subplots. Here, changes in abundance are determined by extinction and colonisation processes which are dependent on the number of occupied subplots in the previous observation period.

To estimate colonisation and extinction rates for this model from the survey data, I define them as

$$logit(c_i) = \gamma_i + \beta_i p_{i,t} \tag{3}$$

$$logit(e_i) = \delta_i \tag{4}$$

Here, I use the logit transformation to ensure that both rates are always constrained to be between 0 and 1. For colonisation, the parameter γ_i captures immigration from outside the transect whereas the parameter β_i allows for immigration between subplots within the transect; and hence is proportional to current occupancy. For extinction, the parameter δ_i represents a species' rate of local extinction. Importantly, present model allows for variation between observations to be driven by flux into and out of the subplots, but without any dependence on the abundance of co-occurring species (no species interactions). Note that the traditional TIB model only allows immigration from the outside, whereas the classic Levins model only allows for colonisation from within the transect.

All following models are variations on a more complex version of the *no interactions* model. In these models, I allow for competitive or facilitative interactions between species to help drive population dynamics within sites but in two distinct ways. In both models, I add an interaction term ($I_{i,t}$) which encapsulates both interaction strengths and the abundance of co-occurring species. In the *colonisation* model (Eq. 5), interactions with co-occurring species can limit the colonisation of new patches such that:

$$logit(c_i) = \gamma_i + \beta_i p_{i,t}(1 - I_{i,t}) \tag{5}$$

More specifically, interactions can affect the immigration rate between subplots within a transect (β_i). The extinction rate and immigration from outside the transect are unaffected by species interactions.

In the *extinction* model (Eq. 6), interactions no longer affect colonisation but can instead affect the extinction rate such that:

$$logit(e_i) = \delta_i + p_{i,t} I_{i,t} \tag{6}$$

Here, it is the rate of extinction within previously occupied subplots which is affected by co-occurring species, while colonisation remains unaffected. The difference between how interactions appear in the *colonisation* and *extinction* models is driven by the fact that interactions effects in the latter must be proportional to current occupancy.

Variants of modelling competitive interactions

Using the models presented above, I ask two questions: does adding species interactions improve predictions of population dynamics, and is there more evidence to support the idea that those interactions affect the colonisation or extinction rate of populations. I can further explore how best to encapsulate the effects of species-species interactions by imposing different constraints on the interaction term $I_{i,t}$ (Eq. 5 and 6). $I_{i,t}$ is composed of the abundances of co-occurring species, $\sum_j p_{j,t}$, and the interaction strength between co-occurring species and the focal species i, α. One possibility is that all species interacting with a given species i have the same interaction strength — in other words, neighbour identity does not matter to i, but neighbour abundance does. This can be captured by a single α value which is identical across co-occurring species, essentially averaging interaction effects across the community (Levine and HilleRisLambers, 2009; Godoy and Levine, 2014). It is alternatively possible that both the identity and abundance of neighbours matters to i, as each species can have a different effect on the focal species i (for example, see Adler et al., 2010). This calls for a unique α parameter for each co-occurring species. Somewhere between these two possibilities, perhaps it is sufficient to group neighbours according to their effect on i. In the latter case, one could suggest conspecifics and heterospecifics have different interactions strengths with i, and assign one α to each group (as in Detto and Muller-Landau, 2016). The following section describes the 3 ways in which I chose to vary the interaction term $I_{i,t}$ in Equations 5 (*colonisation*) and 6 (*extinction*). Note that Table 1 lists the specifics of all candidate models.

identical alphas At it's simplest, I can assume that all other species affect i in the same way such that the abundance of co-occurring species determines the strength of the interaction, rather than the identity of those species. In this formulation, the interaction coeffi-

cient α is specific to a focal species i only, such that

$$I_{i,t} = \alpha_i p_{i,t} \sum_j p_{j,t} \tag{7}$$

two alphas Density-dependant processes are, however, known to regulate population dynamics (Chesson, 2000). It can hence be argued that a focal species will be affected differently by conspecifics than it would be by heterospecifics. Under these assumptions, interactions with i can be captured by two separate interaction coefficients depending on whether co-occurring plants belong to the same species as i or not. In this case,

$$I_{i,t} = \alpha_{ii} p_{i,t} + \alpha_{i.} \sum_{j \neq i} p_{j,t} \tag{8}$$

where α_{ii} is the interaction strength between i and its conspecifics, and $\alpha_{i.}$ is the interaction strength with all other co-occurring species.

unique alphas To relax model assumptions even further, I can assume that every co-occurring species has a different effect on focal species i, determined by both the abundance and identity of the co-occurring species. In this final variant, every co-occurring species including conspecifics is allowed their own interaction coefficient, such that there is one coefficient per pairwise interaction with i. Interactions can be modelled by

$$I_{i,t} = p_{i,t} \sum_j \alpha_{ij} p_{j,t} \tag{9}$$

where I refer to the sum of the interaction coefficients α_{ij} with all individuals of species i and j. This formulation is perhaps the most biologically realistic but its complexity requires by far the most data to resolve compared to the other models described above due to the large number of terms involved (Table 1).

Model name	Full formulation	$logit(c_i)$	$logit(e_i)$	Number of parameters per focal species
random walk	$p_{i,t+1} \sim p_{i,t}$	—	—	1
no interactions	$p_{i,t+1} = p_{i,t} + c_i(1 - p_{i,t}) - e_i p_{i,t}$	$\gamma_i + \beta_i p_{i,t}$	δ_i	3
identical alpha (colonisation)	$p_{i,t+1} = p_{i,t} + c_i(1 - p_{i,t}) - e_i p_{i,t}$	$\gamma_i + \beta_i p_{i,t} \left(1 - \left\{\alpha_i p_{i,t} \sum_j p_{j,t}\right\}\right)$	δ_i	4
two alphas (colonisation)	$p_{i,t+1} = p_{i,t} + c_i(1 - p_{i,t}) - e_i p_{i,t}$	$\gamma_i + \beta_i p_{i,t} \left(1 - \left\{\alpha_{ii} p_{i,t} + \alpha_{i.} \sum_{j \neq i} p_{j,t}\right\}\right)$	δ_i	5
unique alphas (colonisation)	$p_{i,t+1} = p_{i,t} + c_i(1 - p_{i,t}) - e_i p_{i,t}$	$\gamma_i + \beta_i p_{i,t} \left(1 - \left\{p_{i,t} \sum_j \alpha_{ij} p_{j,t}\right\}\right)$	δ_i	56 to 136, depending on site
identical alpha (extinction)	$p_{i,t+1} = p_{i,t} + c_i(1 - p_{i,t}) - e_i p_{i,t}$	$\gamma_i + \beta_i p_{i,t}$	$\delta_i + p_{i,t} \left\{\alpha_i p_{i,t} \sum_j p_{j,t}\right\}$	4
two alphas (extinction)	$p_{i,t+1} = p_{i,t} + c_i(1 - p_{i,t}) - e_i p_{i,t}$	$\gamma_i + \beta_i p_{i,t}$	$\delta_i + p_{i,t} \left\{\alpha_{ii} p_{i,t} + \alpha_{i.} \sum_{j \neq i} p_{j,t}\right\}$	5
unique alphas (extinction)	$p_{i,t+1} = p_{i,t} + c_i(1 - p_{i,t}) - e_i p_{i,t}$	$\gamma_i + \beta_i p_{i,t}$	$\delta_i + p_{i,t} \left\{p_{i,t} \sum_j \alpha_{ij} p_{j,t}\right\}$	56 to 136, depending on site

Table 1: All model formulations and number of parameters.

Estimating model coefficients

The eight candidate models consisted of the *random walk* (Eq. 1), the *no interactions* model (Eq. 2), and the interaction variants for both the *colonisation* (3 models, following Eq. 5) and the *extinction* (3 models, following Eq. 6) rate. Each model variant was implemented for every species at each site, for a total of 261 species $\times$ site combinations. I treated each site as representative of a single community. Consequently for each of these combinations, I considered a competitor to be any species that was recorded at any time in the same site, regardless of whether it was present in the same transect as the focal species. The number of potential competitors per species i (including conspecifics) varied from 53 to 133, depending on the study site.

Given the complexity of the different model variants, I adopted a Bayesian approach to estimate best fit parameters even for the highly parameterised options (Eq. 9). To do so, I used the rjags and R2jags packages in R with the glm module (Plummer, 2003; Su and Masanao, 2012; R Development Core Team, 2016). Parameters for each species and model variant were estimated independently by using a Markov Chain Monte Carlo algorithm to sample their probability distribution. The algorithm works by constructing several Markov chains which iteratively sample from the expected target distribution of each parameter.

Each model was run with three chains and 300 000 iterations, and I discarded the first half of the chain. Of the remaining 150 000 iterations, I drew samples every ten iterations to construct the parameter posterior distributions. The β, γ, δ and α parameters were all given uninformative prior distributions. Their sign was unconstrained, which in the case of the α's allows for negative or positive values as interactions between plants are not necessarily competitive (Grace and Tilman, 1990).

I verified each chain for convergence to the target distribution, suitable chain length and autocorrelation between chain steps with the coda package (Plummer et al., 2006). These tests included the Gelman-Rubin statistic, which verifies whether parallel chains converge to the same target distribution (Cowles and Carlin, 1996), and the Geweke test which checks the Markov chain is a stationary process and has run the necessary amount of time. Note that the above tests are indicative only as one cannot determine with absolute certainty whether a sample taken from a MCMC process is representative of an underlying stationary distribution (Cowles and Car-

lin, 1996). Rather, each of the tests can help identify different issues which may arise from running each model. This implies that a given test may indicate nonconvergence even when other tests pass without issue. This is especially common when posterior distributions are multi-modal, as different chains may converge on different targets within a distribution and fail between-chain convergence diagnostics (Woodard and Rosenthal, 2013). This was not altogether uncommon in my analyses, I therefore permitted final models to fail certain validation tests as long as a minimum of one test was validated. Failure to reach convergence was not specific to species or site. Models that failed all tests were discarded, accounting for 8.1 % of all models. Overall the *random walk* and *no interactions* models converged the best. Out of the models which included interaction terms, the simplified and constrained versions had reached convergence less often than the final, complex model forms (Figure 3).

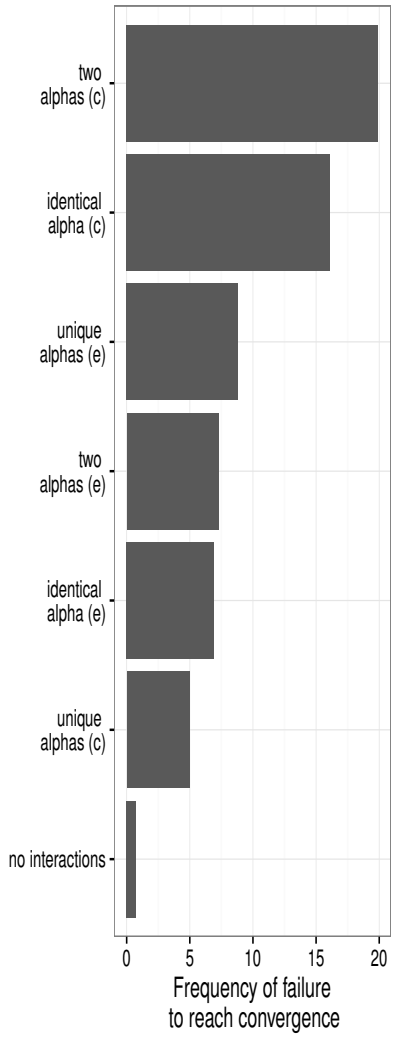

Figure 3: Frequency of model variants which failed convergence, in % of total number of models run ($N = 2088$).

For those estimates that satisfied the above criteria, I compared model formulations using the Deviance Information Criterion (DIC), a Bayesian model equivalent to the Akaike Information Criterion (AIC) (Spiegelhalter et al., 2002). Similar to AIC, DIC is an estimation of model fit based on deviance that includes penalties for increasing the number of parameters; as such, a lower DIC signifies a better fit. As a rule of thumb, a difference in DIC of 3 or more suggests one model predicts the data significantly better than the other (Spiegelhalter et al., 2002). Based on those DIC values, I estimated the best fit model formulation for each of the 261 species $\times$ site combinations. I also calculated differences in DIC in two ways, first $\Delta DIC_{randomwalk}$ as the difference in DIC between each model and the *random walk* for each species $\times$ site, then $\Delta DIC_{bestfit}$ as the difference in DIC between each model and the best fit model for that same species $\times$ site. Models with lower ΔDIC values of either type show a better fit to the data. For each species $\times$ site, I ranked the models by lowest DIC. Models which had a difference of 3 DIC or less were given an equal rank, that of the minimum of the two rankings.

Results

Support for different model formulations

Changes in focal species abundance for 255 out 261 total species × site combinations were best explained by a model that included interactions with co-occurring neighbours (Figure 4). Formulations that did not allow for an effect of interactions, *random walk* and *no interactions*, provided the best fit for the six remaining species × site combinations. Though the *no interactions* model performed marginally better than the *random walk*, neither performed well (Figure 4). Regardless of whether interactions were associated with the colonisation or extinction rate, the *identical alpha* and *two alphas* formulations were supported by 45 and 52 species × sites respectively. Out of all the candidate models, the *unique alpha* formulation with one α per pairwise interaction had the best predictive ability for the remaining 159 species × sites, despite having by far the most absolute model parameters (Table 1, Figure 4).

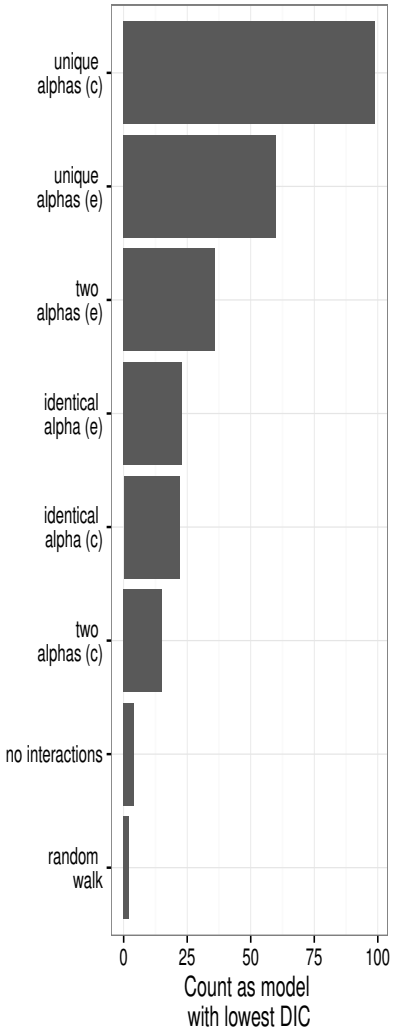

Figure 4: Models sorted by lowest DIC. The x axis refers to the number of species × site for which a certain model formulation has the lowest DIC, out of the total 261 species × sites. Models which failed convergence were not included.

When examining results over the whole dataset, differences in DIC between each model variant and the *random walk* over all species × sites were not significantly different to each other (Figure 5), though the range of DIC values between species × sites was large (0.2 to 7116.4) and could confuse the results. Similarly to other likelihood-based methods of model comparison, DIC is relative to a dataset but not to the amount of variation within the data. This means comparisons cannot be drawn between species or sites, only between model variants.

The interquartile range of $\Delta DIC_{randomwalk}$ values for both *unique alphas* models was below -3, indicating a significantly better fit than the *random walk* (Figure 5). This was also the case for the *identical alpha* and *two alphas* variants where interactions affect the extinction rate. Differences in DIC between each model variant and the best fit model show a similar pattern (Figure 6), with the range of values overlapping between each model. The interquartile ranges of $\Delta DIC_{bestfit}$ for both models with no interactions are above 3, which indicates they tend to be significantly worse than the best fit model. The interquartile ranges of both *unique alphas* models, however, show the smallest difference in $\Delta DIC_{bestfit}$ values, indicating that those models tend to have DIC values close or equal to the best fit model.

For each model, I calculated its mean and median ranking across all species × site combinations (Table 2, first column). Mean and median rankings were not significantly different from each other,

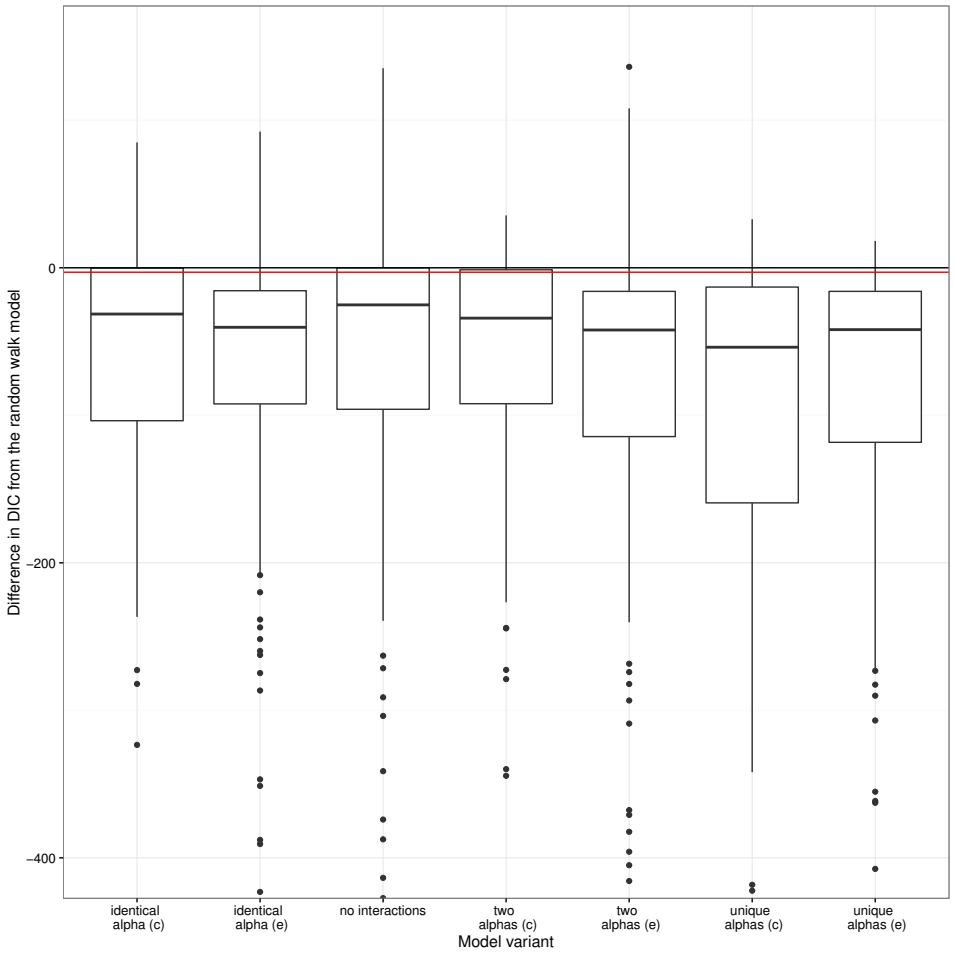

Figure 5: Differences in DIC between each model variant and the *random walk* model, by species × site. A value of 0 means the model has the same DIC as the random walk. Model performance is regarded as significant when the difference in DIC is of 3 or more. The red line has an intercept of −3, any model below the line is a significantly better fit to the data than the random walk model. Extreme outliers were removed across models for clearer presentation.

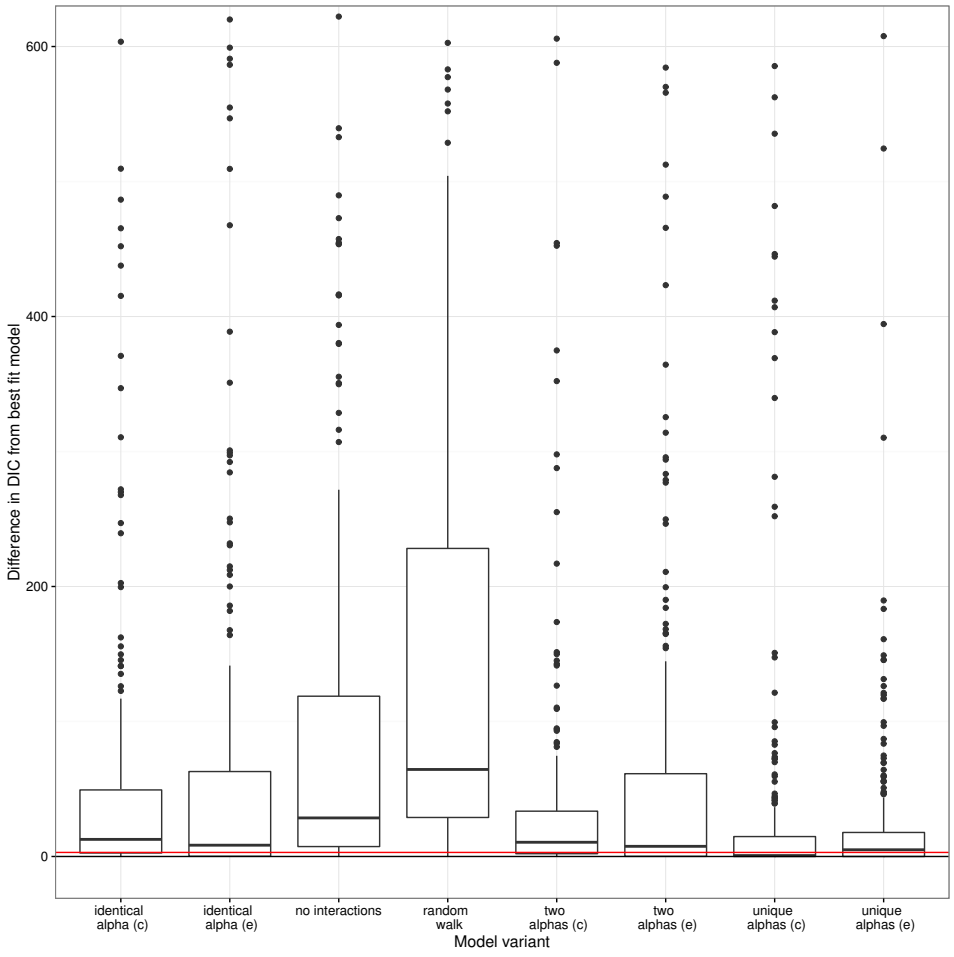

Figure 6: Differences in DIC between each model variant and the best fit model, by species $\times$ site. The red line indicates the cutoff for a significant difference in DIC. Note that a value of 0 indicates that these particular model variants showed the best fit to the data. Extreme outliers were removed across models for clearer presentation.

Median model ranking over all sites		Median model ranking by site		
		Earnscleugh	Galloway	Mavora
all alphas (c)	1	1	1	2
all alphas (e)	2	3	3	1
common alphas (e)	2	3	3	1
dual alpha (e)	2	3	3	1
common alphas (c)	3	3	4	3
dual alpha (c)	3	3	4	3
no interactions	4	4	5	4
random walk	6	6	6	7

Table 2: Table of median ranking for each model formulation overall and according to site.

so I report here the median as it provides a clearer picture. Median model rankings show the same pattern as that observed in Figure 5, with the colonisation variant of *unique alphas* ranked first across all species and sites, followed by the other interaction models. The *random walk* and *no interactions* variants were ranked last and second-to last, respectively, across all sites.

Among the species $\times$ sites where a model with interactions performed best, the split between placing interactions in the colonisation or the extinction rate was fairly even (Figure 4) across all model variants. The *unique alphas*, colonisation model, however, performed best overall and provided a better fit for 39 species $\times$ sites, more than the *unique alphas* extinction models. Among the simplified *identical alpha* and *two alphas* interaction models, placing interactions within the extinction rate gave a better predictive ability than placing them within the colonisation rate (Figure 4 and Table 2). Granted, differences in ΔDIC were not significant between each of the colonisation or extinction variants (Figures 5 and 6).

Differences between sites

Species richness and composition varied from site to site, with the least diverse site containing 53 unique common species and the most diverse, 133 species. Site species richness was strongly correlated with the number of transects present (*cor* = .99), but not with the number of observations. The sites were also spread across an elevational gradient. Sites at lower elevations were dominated by exotic species, whereas the higher elevation site was native-dominated, with a high prevalence of shrubs and tussock grasses, that are typically longer-living and slower-growing than the dominant forbs and grasses species of the lower elevation sites (Moore, 1955).

Model performance between each site was similar overall (Figure 7), with the *unique alphas* formulations returning lower DIC values for more species than any other variant. The variants with no interactions universally performed worst, and the simplified interaction variants performed slightly better. Both model forms without interactions ranked last for all sites (Table 2).

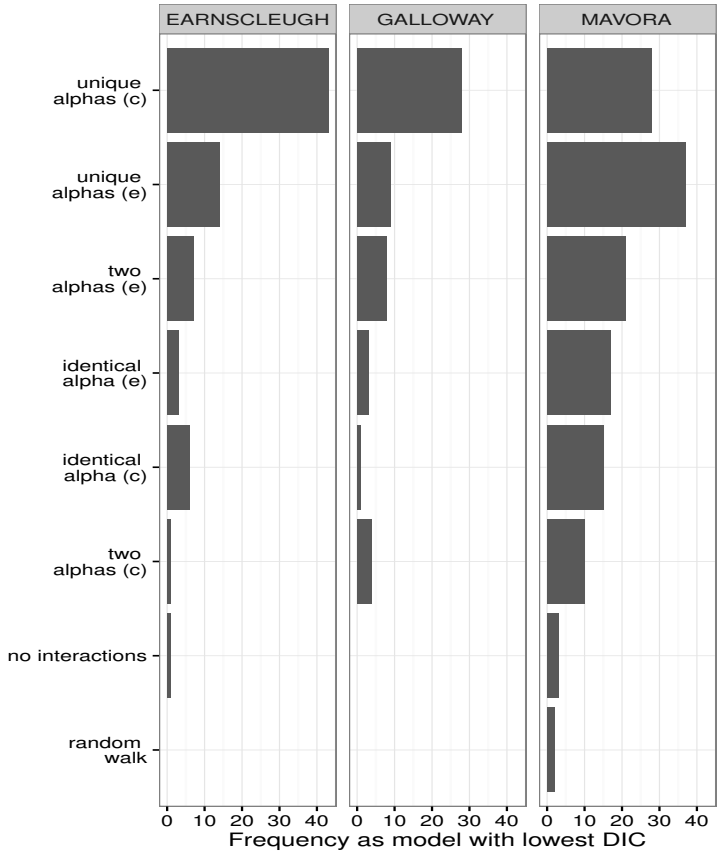

Figure 7: Models sorted by lowest DIC for each location. Frequency is given as the % of the total number of models run for each site which has reached convergence ($N_{Earnscleugh} = 510, N_{Galloway} = 382, N_{Mavora} = 1027$).

Sites differed on whether interactions were best placed within the extinction or the colonisation parameter. There was stronger support for the interaction-term associated with colonisation at the Earnscleugh and Galloway sites, while the opposite was true for Mavora (Table 2). Mavora was the only site for which the colonisation variant of *unique alphas* was not the overall best fit, with the extinction variant receiving more support instead. Nonetheless, the *unique alphas* was still one of the best models at Mavora and the two *unique alphas* models consistently received the lowest DIC values for a majority of species at all sites.

Model parameters & interaction coefficients

To better understand what was driving the differences in model performance between sites, I investigated the parameter values representing immigration and extinction processes in the best supported *unique alphas*, colonisation model. Given that patterns of interaction strength are tied to community structure and stability, I also asked whether there was any variance in the overall patterns of interaction strengths between sites, and if those differences could be related to differences in community composition. Only parameters from the *unique alphas* colonisation variant were selected, given that is was the overall best model and there was a strong and significant correlation in interaction parameter values between the extinction and colonisation variants of the *unique alphas* model at each site (Earnscleugh = .74, Galloway = .70, Mavora = .62, all $p < 0.001$). To represent parameter values, I selected the median as a point estimate for each parameter, as it is less susceptible to being skewed by outlier values than the mean. I only selected those models for species $\times$ site combinations that had fully converged, giving us parameter estimates for 248 species $\times$ sites.

I found possible trade-offs occurring between the values of the β, γ and δ parameters (Figure 8). Overall, the rate of immigration from outside the transect (γ) decreased with increasing immigration between subplots. At the Mavora site however, immigration between subplots was close to 0 for many species, with colonisation driven mainly by immigration from outside the transect. Moreover, colonisation from outside the transect (γ) showed an increase with local extinction rate for both the Earnscleugh and Galloway sites, but not for the Mavora site. As γ is not directly affected by interactions in the *unique alphas*, colonisation model, this could explain why the extinction rate variant performed better at this site.

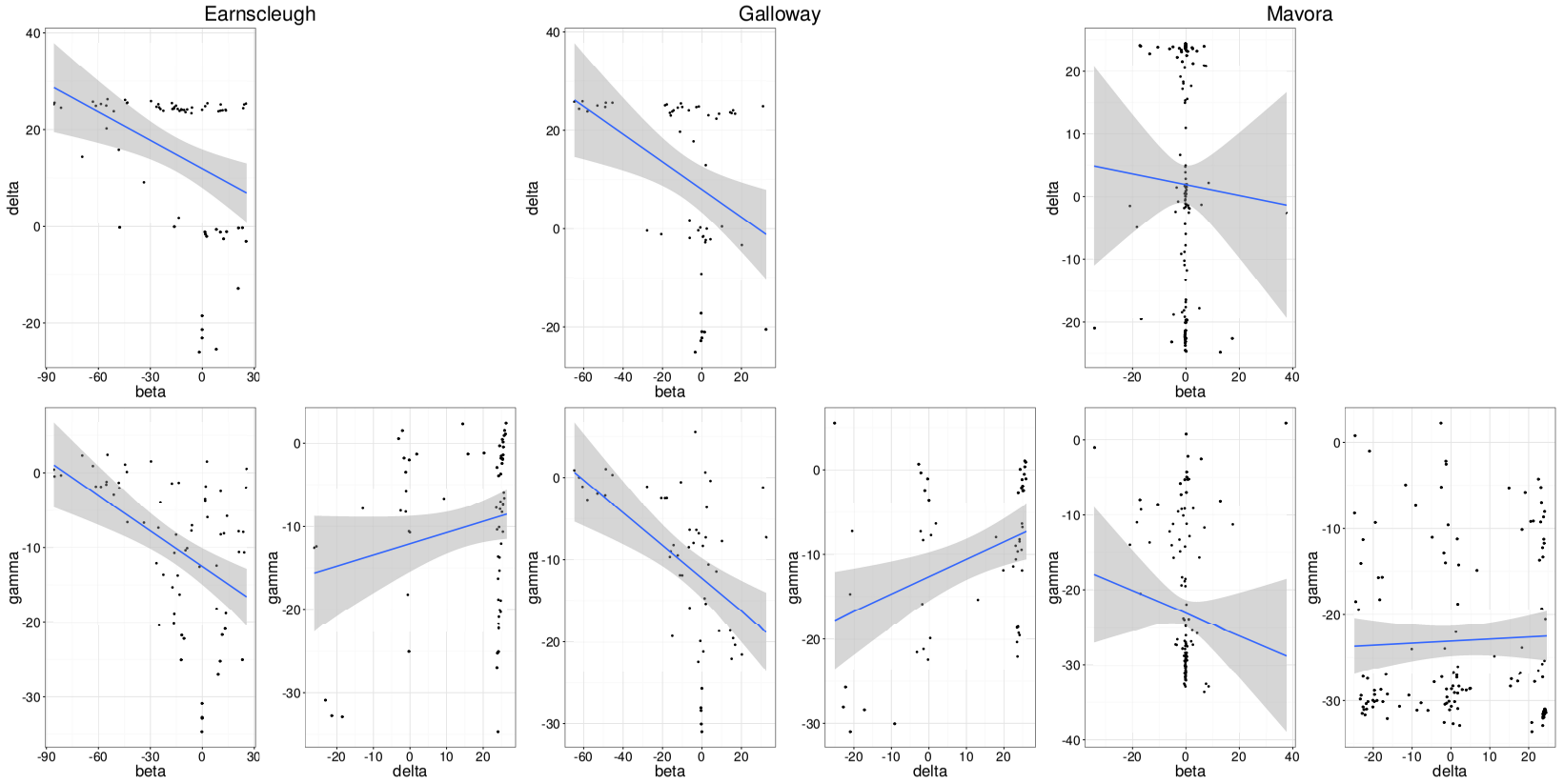

Figure 8: Joint distributions of non-interaction parameter values for the best supported model (*unique alphas* colonisation), by site. Parameter point estimates are taken from the median value of the posterior distributions. The lines were fitted using a linear regression, the shaded areas correspond to the 95% confidence intervals.

Overall, median values for the α parameters in the *all alphas (c)* models were strongly aggregated around 0 (Figure 9). Interaction strengths at the Mavora site showed higher clustering at 0 than Earnscleugh or Galloway. Differences in the variance of interaction strength distributions at each site were strongly significant (Levene test, $p < 0.0001$). Mean interaction strength at Earnscleugh and Galloway was slightly negative, indicating an overall facilitative effect.

Each value of interaction strength in the *unique alphas* model is specific to a focal species and one interaction partner at a given site. I therefore investigated interaction strength distributions from the point of view of each focal species at a given site ($n = 248$), and each interaction partner at a given site ($n = 260$). In the majority of both cases, the distribution of interaction strength mirrored that of the overall α distribution.

Of the 248 focal species $\times$ site combinations, 51 had an α distribution significantly different to the overall *all alphas (c)* α distribution. Of the 260 interaction partner $\times$ site combinations, 34 had an α distribution significantly different to the overall distribution. Fifteen species $\times$ site combinations appeared in both groups, either as a focal species or as an interaction partner. Some species showed a significantly different α distribution across several sites. Of the 51 species which had a significantly different α distributions either as a focal species or as a competitor, 33 were forbs and 34 were exotic species.

The number of focal species and interaction partners with an α distribution significantly different from the overall α distribution, was in itself significantly higher than expected at both the Earnscleugh and Galloway sites ($x^2 test, p < 0.0005$). Conversely, the number of interaction partners with an α distribution significantly different from the overall α distribution was lower than expected at the Mavora site ($p \sim 0.01$). I selected the mean α value of each species $\times$ site and each interaction partner $\times$ site combination. The mean α values of species or interaction partner $\times$ site combinations with a significantly different α distribution were significantly weighted towards negative values ($x^2 test, p < 0.0005$), indicating facilitation.

I grouped species by exotic or native status, and compared α values with co-occurring species in either the same or opposite groups (Figure 10). The distribution of these interaction strengths were significantly different between all groups and across all sites (Levene tests, all p values were < 0.001). For the Earnsleugh and Galloway

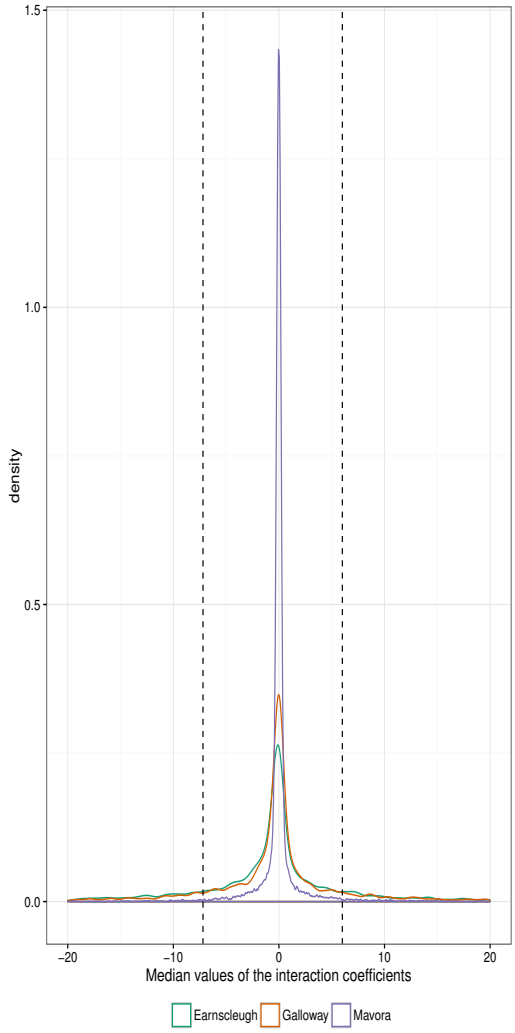

Figure 9: Density distribution of the α_{ij} parameters in the *unique alphas (c)* models, by site. Mean interaction strength at each site (μ) were the following: $\mu_{Earnscleugh} = -0.97$, $\mu_{Galloway} = -0.68$, $\mu_{Mavora} = 0.01$. Extreme values ($|\alpha_{ij}| > 20$) were removed from the figure for clarity. The area between the dotted lines covers the 5th to 95th quantiles of all α_{ij} values.

sites especially, it is visually apparent that native species interacting with natives had a more restrained distribution of α values. Exotic species interacting with either natives or exotics showed a much wider distribution in their α values, indicating stronger competitive or facilitative interactions.

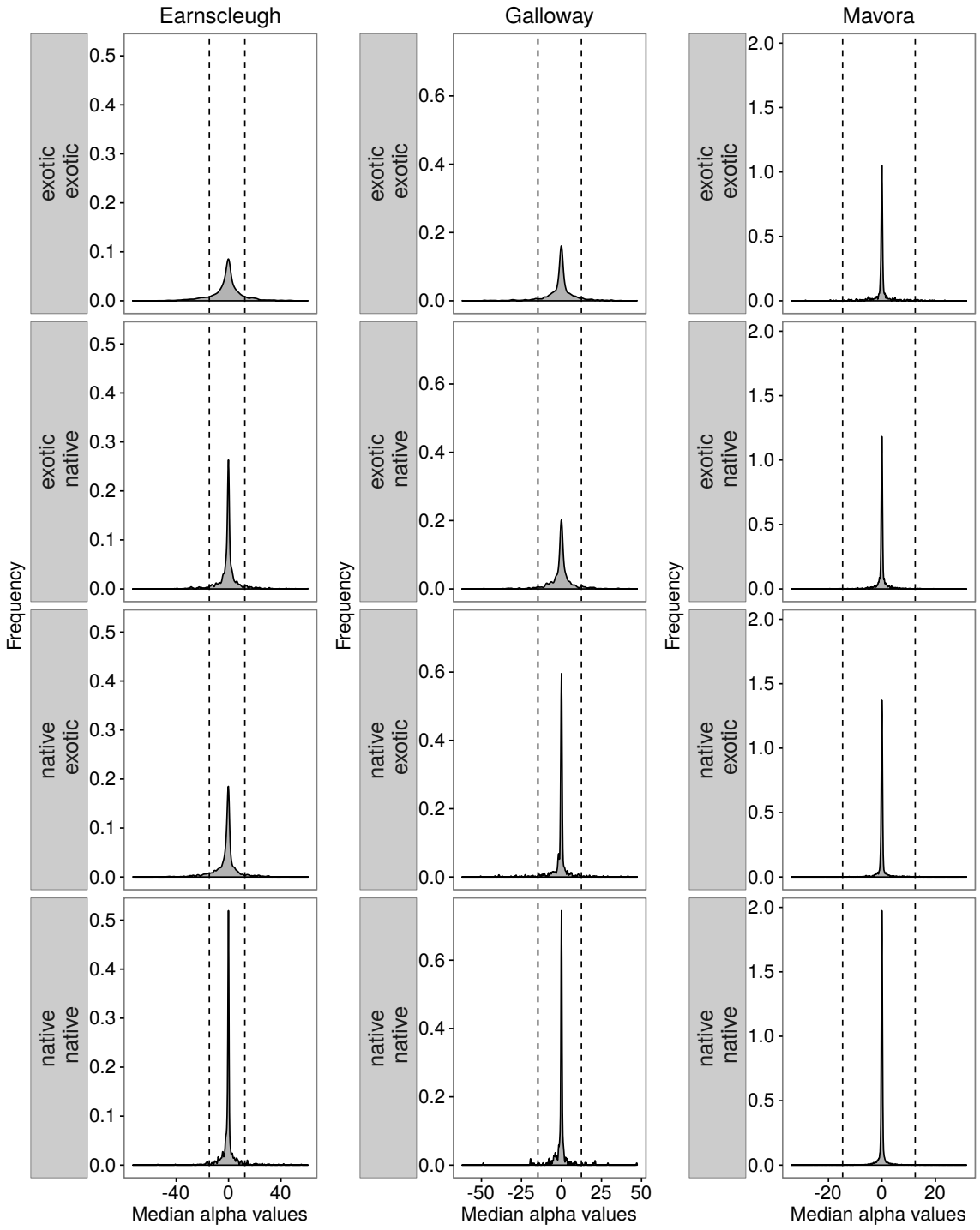

Figure 10: Distribution of interaction strength values between groups of exotic and native plants, for each site. The area between the dotted lines covers the overall 5th to 95th quantiles. Note the use of different scales on both axes for each site.

Discussion

Across 261 species × site combinations, the inclusion of species interactions improved predictions made by population dynamic models 98% of the time. Model predictions improved with each step towards a more complex and biologically meaningful formula, regardless of which process (extinction or colonisation) included the interaction term. The most successful model (*unique alphas*) allowed for variation in both interaction sign (facilitation or competition) and strength for every pairwise interaction. In this latter model, the distribution of interaction strengths was skewed towards larger values at lower elevation sites, and weaker interactions at the high elevation site. When interacting with each other, exotic species showed a wider distribution of interaction strengths than native species.

Quantifying pairwise interactions

Interactions between plants significantly contributed to the observed variation in population dynamics for an overwhelming majority of species in this study. Modelling every pairwise interaction in a natural grassland community is a complex task, but this approach can strongly inform predictions of population dynamics, and in turn allow us to draw inferences on community stability as described further below. Hopefully these results will also impact future studies modeling grassland population dynamics: generalising interaction effects across the community is an improvement over ignoring interactions, but no substitute for estimating every pairwise interaction strength. This latter point does not suggest that all species in a community meaningfully interact with each other, but rather that the strength and significance of interactions is dependant on both the identity and abundance of the interaction partners.

In this study, my approach to modelling interactions was rather 'naive' as the priors assigned to the interaction coefficients were uninformative. However, one benefit of adopting a Bayesian framework is that knowledge of interactions, such as which species are more likely to interact, drawn from the literature, plot experiments or even studies such as this one can be incorporated into the model by assigning informed interaction priors (Ellison, 2004). Additionally, the posterior interaction strengths estimated here can be used to inform future models of plant interactions. This provides a way forward in unifying results from different studies into the same model framework.

Distribution of interaction strengths

A major benefit to modeling every pairwise interaction is that it allows the estimation of all pairwise interaction strengths, which have been linked to community stability (Tang et al., 2014) and niche differences (Adler et al., 2007). Stable communities are predicted to have a high number of weak interactions and a few strong ones (Paine, 1992; Polis and Strong, 1996; Kokkoris et al., 2002; Neutel et al., 2002), in part because weak interactions limit the spread of negative effects such as extinction cascades throughout a community (Wootton and Emmerson, 2005; Fowler, 2010). In this study, the overall distribution of interaction strengths in the best predictive model (*unique alphas* colonisation) followed this pattern with a high density of weak interactions. This distribution did however vary from site to site, indicating some differences in the structure and stability of each community.

The variance of interaction strengths in each community was significantly different, and the density of weak interactions increased with elevation. This suggests community stability increased with elevation in this study. Plant communities at higher elevations are not necessarily more inherently stable, but are subject to harsher environmental conditions such as cooler temperatures and low soil moisture. They have been hypothesised to be more heavily regulated by environmental factors, rather than interactions (Grime, 1977). As plant communities increase in elevation, they are hypothesised to experience a weakening of competition and an increase in neutral or facilitative interactions, according to the stress-gradient hypothesis (Bertness and Callaway, 1994; Callaway, 1995; He et al., 2013). The mean interaction strength of each community did not differ significantly, but the increase in weak interactions could be attributed to the higher abiotic stress experienced by the Mavora community.

The increase in weaker interactions observed in the Mavora community could also be related to differences in its composition. This community was dominated by native species, in contrast to the lower elevation communities which were dominated by exotics. Native species interacting with natives had a higher distribution of weak interaction strengths than exotics interacting with other exotics or natives. Some native species in New Zealand grasslands have been shown to experience fewer changes in frequency and abundance than exotic species (Walker, 2000), which could reasonably translate to an observation of weaker interaction effects. Furthermore, in invaded communities, some exotic species are thought to be stronger com-

petitors relative to native species for a variety of reasons including higher growth rates, release from herbivore pressure, and having fewer competitors (Callaway and Ridenour, 2004; Vila and Weiner, 2004; Riley et al., 2008; Porté et al., 2011; Parker et al., 2013; Zheng et al., 2015). In some cases, interactions between exotic species have also been shown to be strongly positive, facilitating subsequent invasions (Simberloff and Holle, 1999; Rodriguez, 2006; Montgomery et al., 2012). Hence, the exotic species dominating the lower elevation sites could also have contributed to the wider range of interaction strengths observed in those communities, and a decrease in their overall stability.

Additionally, exotic species overwhelmingly belonged to the forb or graminoid guilds. Native species, on the other hand, included more members of other guilds such as shrubs or sub-shrubs. Species belonging to the same guild share some overall similarities in traits and life-history trade-offs (Diaz et al., 1997), such as stress-tolerance versus competitive ability (Grime, 1977). The tendency for strong interactions displayed by exotic species might hence be a reflection of forbs and graminoids having strong interaction effects; whereas the majority of weak interactions between native species could be due to members of other guilds, such as shrubs or subshrubs, experiencing weaker interactions than forbs or graminoids. Functional traits have been shown to successfully predict interaction intensity in some cases (Kunstler et al., 2012; Fortunel et al., 2016) and could be used to further explore this variation in interaction strengths.

Study limitations

One potential issue with the dataset used in this study is that the Mavora site was only sampled twice, which might not have fully captured the breadth of variation in plant abundances over a season, and led to an overestimation of the stability of the system. Other limitations of this study concern the posterior distributions of each interaction strength, which overlapped 0 in the majority of cases. This was likely due to the majority of parameter posteriors showing a multi-modal distribution, which could suggest some trade-offs occurring between positive and negative parameter values. Constraining the parameter priors did not improve parameter estimation. This issue is perhaps not surprising given that the dataset was zero-inflated and contained much colinearity between the abundances of co-occurring species, a caveat of using observational data. Unfortunately the presence of multi-modal distributions can complicate measures of model comparison, including DIC, though alternatives

robust to multi-modality can be computationally expensive and are still being explored (Hooten and Hobbs, 2015). Nevertheless, differences in model performance were rather striking and consistent over a large number of species $\times$ site combinations, which has led me to feel confident in the robustness and insightfulness of my approach.

Conclusion

Estimating every pairwise interaction strength in a natural grassland community is feasible given sufficient observational data, and improves predictions of plant population dynamics. This confirms the importance of biotic interactions in shaping plant community composition and patterns of abundance, and suggests species identity is as relevant as abundance in determining the effect of one species on another. I am led to caution future studies exploring population dynamics against ignoring or oversimplifying the effect of species interactions (Nylén et al., 2013). Additionally, this method uncovered significant differences in the distributions of interaction strengths between communities and groups of species. Interactions were weaker between native species than between exotics, and the density of weak interactions increased with elevation regardless of the species' biological status. This suggests multiple factors are responsible for differences in the overall distribution of interactions between communities.

Given that this pairwise approach explicitely estimates interaction strengths between species, it provides a starting point for several lines of investigation comparing these measures, such as the relative importance of competitive versus facilitative interactions or how interactions might vary along environmental conditions. Measures of interaction strengths can be reflective of niches differences (Adler et al., 2007) and community response to disturbances (McCann et al., 1998), thus providing insights into mechanisms of community coexistence (Mayfield and Levine, 2010) and stability (Tang et al., 2014). By identifying interaction partners, this approach can also guide constraints on future models of interacting plant species (Wootton and Emmerson, 2005), and can lead us to represent these communities as a network, opening them up to application of analyses borrowed from the graph theory toolbox (Strogatz, 2001; Dunne et al., 2002; Pavlopoulos et al., 2011).

How plant interactions vary by guild and along two abiotic gradients

Abstract

Species interactions vary as a function of species identity and environmental conditions. This context dependency makes it difficult to generalise the outcome of interactions between communities. Several ideas, including the stress-gradient hypothesis, have been put forward to describe how interactions might vary along abiotic gradients. Such patterns are, however, not always supported by observational data. Furthermore, studies exploring variation in interaction strength are generally limited in both the number of species and the number of abiotic gradients observed. Our understanding of how interactions vary within a realistic context is therefore far from complete. Here, I explore the context dependency of interaction strengths in natural, highly diverse grassland communities from New Zealand. I average the effects of interactions across four plant guilds and allow them to vary along two abiotic gradients, elevation and latitude. Such a model improves predictions of plant population dynamics compared to models which include only interactions, or only abiotic factors. I then explore how elevation and latitude affect the interaction strengths with each plant guild. I find that both gradients increase facilitation between focal species and forbs, but weaken interactions and lowers facilitation with graminoids and woody species. The relationships between interactions and abiotic gradients are hence complex and strongly dependent on the characteristics of the interaction partner.

Introduction

In plant communities for example, a species can compete with or facilitate the growth of another. These interactions, along with environmental variation, can drive patterns of both species abundances and distributions. In order to quantify how species affect each other,

we can estimate interaction strength as the per capita effect of one species on another (Laska and Wootton, 1998). Both the sign and intensity of this interaction strength can be highly variable, depending on its biotic and abiotic context (Thompson, 1988). Interactions and environmental effects have long been studied in ecology, but our understanding of the simultaneous impact of the two is still incomplete (Chamberlain et al., 2014; Mod et al., 2016).

Many studies report variation in pairwise interaction strength under different environmental conditions. In fact, a meta-analysis of studies quantifying variation in species interactions by Chamberlain et al. (2014) found that the greatest variation existed along abiotic stress gradients, rather than across spatial (multiple sites) or temporal scales (data collected over time). This finding was evident across multiple interaction types, including competition and mutualism. For example, the shrub *Retama sphaerocarpa*, suffers from neutral or negative interactions with its associated understorey species in wet, fertile environments. This interaction becomes positive in dry environments (Pugnaire and Luque, 2001). In another study, Pennings and Sillman (2005) found that after controlling for diversity and density, latitudinal differences in interaction strength between herbivores and the salt-marsh plant *Spartina alterniflora* were driving differences in plant palatibility. These examples, and others, support the stress-gradient hypothesis, which suggests that competitive or negative interactions weaken as abiotic conditions become less tolerable (Bertness and Callaway, 1994; Callaway, 1995; He et al., 2013). This hypothesis however, is debated. The strength of species interactions does not necessarily follow a simple pattern across abiotic stress gradients (Maestre et al., 2005, 2006). The issue is further complicated by the fact that species in natural communities typically experience variation along multiple environmental factors at once (Mod et al., 2014), a reality which has rarely been tested explicitly in observational studies (Mod et al., 2016). There are experimental studies of the impacts of multiple abiotic gradients, but these are generally limited in spatial scale or species number (eg. Leathwick and Austin, 2001; Grau et al., 2010).

Interactions are typically mediated by mechanisms acting on a discrete, local scale. In the aforementionned case of the *Retama sphaerocarpa* shrub, variation in interaction strength was caused by changes in the micro-environmental conditions through canopy shading and the accumulation of organic matter in the soil (Moro et al., 1997; Pugnaire and Luque, 2001), both local processes than impact the local environment only. Variation in environmental conditions can also

occur over much broad scales, corresponding to climate or elevation. Correspondingly, the effect of interactions between species, even when based on local mechanisms, can be observed at larger, regional scales (Gotelli et al., 2010; Wiens, 2011) as is evidenced by the drive to include biotic interactions in order to improve species distribution models (Leathwick, 2002; Meier et al., 2011; Meineri et al., 2012; Kissling et al., 2012; Welk et al., 2014). There is hence a need to explore how the context-dependency of interactions might affect distribution patterns at a landscape or broader spatial scale.

In addition to operating at different spatial (and temporal) scales, biotic interactions are also expected to vary among species with distinct life history strategies or functional groups. For example, it has been well documented that plants vary widely in water uptake and retention (Mitchell et al., 1993; James et al., 2003). Such functional differences can, in turn, lead to variation in interaction outcomes between plant guilds in response to both environmental gradients and the turn over in neighbourhood species composition (eg. Nylén et al., 2013). Pajunen et al. (2011) illustrate this nicely in their study of Eurasian tundra, in which they found that forbs and graminoids responded differently to increasing shrub cover (driven by climate warming), an effect mediated by changes in the outcomes of species interactions. As plant guilds absorb and utilise resources in different ways, the effects of competition can potentially vary between groups (Peltzer and Köchy, 2001). Studying the combined impacts of species interactions and environmental gradients on individual species is data and computational intensive. Because evidence suggests that groups of species with similar traits related to key interfaces with the abiotic and biotic environment, functional groups, termed 'guilds' here (Walker, 2000), can be used to generalise interaction effects and allow for simplification of plant relationships within a community (Diaz et al., 1997). This approach can be preferable to averaging interaction effects over the whole community as it allows for some variation in interaction strength according to species identity, while making a given model or analysis more tractable and less computationally demanding than, for example, modeling every pairwise interaction.

Here, I explore how interactions between focal species and four guilds (graminoids, forbs, woody species and non-woody others) from natural, diverse plant communities vary with latitude and elevation, proxies for a range of environmental factors. The data used in this study span 20 natural New Zealand grassland sites. I use these data for two purposes.

First, I compare a series of models based on how well they each predict changes in plant abundances. I hypothesise that a model incorporating interactions between guilds that vary along elevation and latitude will improve predictions for the majority of focal species, more so than models including only interactions or only abiotic effects.

After verifying the validity of such a model, I then explore how the interaction strengths between focal species and each guild vary as a function of latitude and elevation. I hypothesise that increasing elevation and latitude will generally weaken the strength of these interactions, as suggested by the stress-gradient hypothesis. However, I also expect interactions with each guild to vary differently along each of those two abiotic gradients.

Methods

Data collection

The data used for this project are plant-abundance time-series from the New Zealand National Vegetation Survey databank (NVS). I selected permanent grassland transects which had been re-measured on a yearly basis with the "species transect frequency" method (STF) detailed in Wiser and Rose (1997), and in the previous chapter. This STF method measures how often a species is present or absent in a series of subplots. Therefore it is not a direct measure of abundance but rather provides an estimate of the probability $p_{i,t}$ of encountering a species i in each subplot at time t. For example, a species with a STF of 0 is absent from all subplots but not necessarily absent from the community, which translates to a very low but non-zero probability of being encountered. Conversely, a species with a STF of 100 is present at all subplots, and hence very likely to be encountered within the community at large. For the purposes of this study, I can assume that variation in the probability of being encountered directly follows variation in abundance, hence all measures of transect frequency were transformed into encounter probabilities. This transformation circumvents some of the issues caused by not having direct measures of abundance.

The final dataset covered 163 transects from 20 sites in New Zealand (see Figure 11). Each site consisted of 4 to 23 transects within a 10 km² area, with each transect measured 2 to 7 times (Figure 12). All data were gathered between 1981 and 1998. Latitude and elevation of each transect was also recorded, with sites covering a range of elevations from 20 to 1600 meters above sea level (Figure 13) and 41 °32′

to 45 °43′ S in latitude. Within site variation in elevation and latitude was also included in the models.

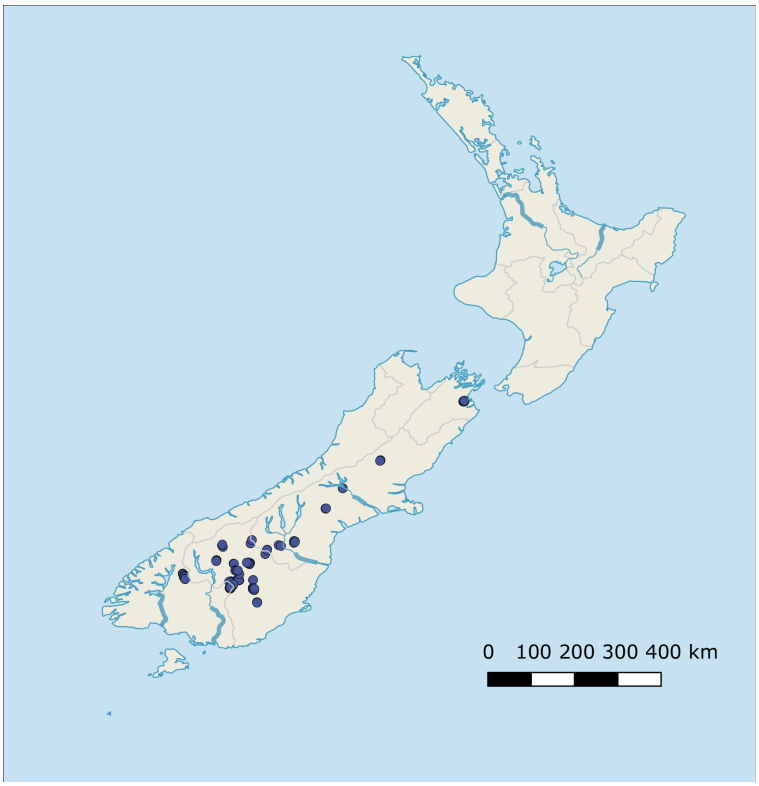

Figure 11: Map of transect locations, each transect is represented by a dot. Many dots are superimposed given that transects within a given site were very close together.

Grasslands can be highly diverse ecosystems. To improve the tractability of my models and work within the limits of my computational capacity, I removed uncommon species (species which always occupied less than 10% of subplots over all observations, $n = 109$) from the dataset, since they are less likely to result in widespread competitive effects (Adler et al., 2013). I then grouped these remaining 339 focal species into four guilds based on their general appearance and growth form, as recorded by the NVS: forbs (f), graminoids (g), woody species (w; this includes shrubs, subshrubs and trees) and non-woody others (o; this includes vines, ferns and non-vascular species). Forbs were the dominant group containing half of all final species (174), followed by graminoids (90) then woody species (64). The misceallaneous 'non-woody other' group only contained 11 species. Given there were so few of them, I grouped them together as distinct from the other three guilds to improve computational tractability, despite obvious differences between members of this group. Uncommon species were evenly distributed amongst guilds ($x^2 = 0.146$).

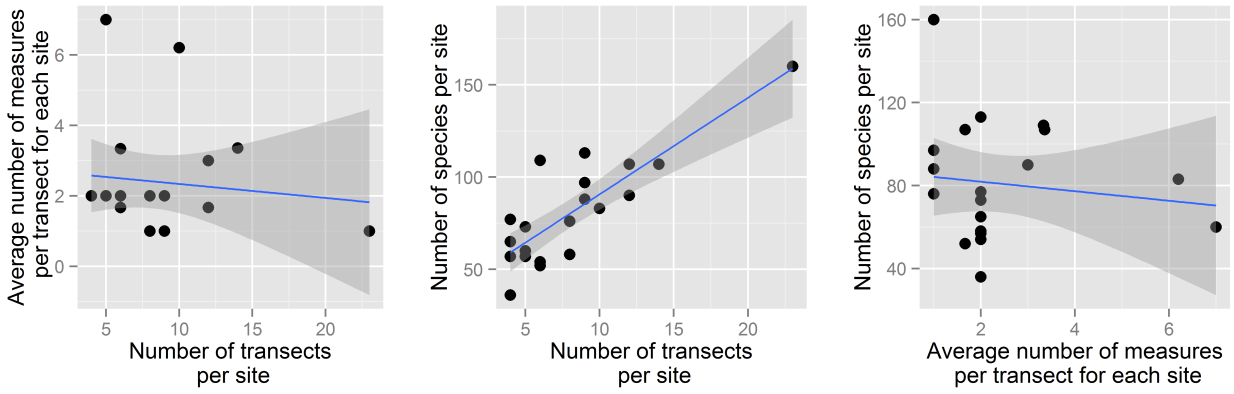

Figure 12: Variability in the number of transects, measures and species at each site. The lines were fitted using a linear regression, the shaded areas correspond to the 95% confidence intervals.

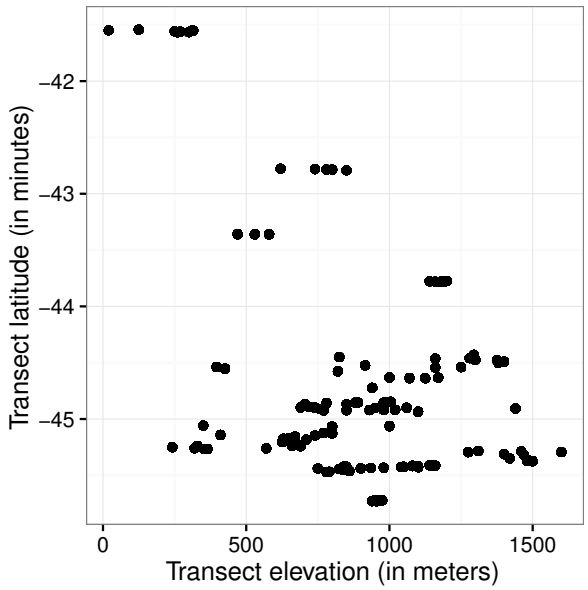

Figure 13: Range of transect latitudes and elevations.

Model framework

To answer my questions, I developed a model framework inspired by Levins' metapopulation model (1970) and the Theory of Island Biogeography Mac Arthur and Wilson (1967) which treat changes in species frequency as the outcome of colonisation and extinction processes acting on the subplots along a given transect :

$$p_{i,t+1} = p_{i,t} + c_i(1 - p_{i,t}) - e_i p_{i,t} \tag{10}$$

where $p_{i,t}$ is the probability of encountering species i in each subplot at time t, c_i is the colonisation rate of species i into unoccupied subplots and e_i is the extinction rate of species i in occupied subplots.

To estimate colonisation and extinction rates from the observed data, I defined them as

$$logit(c_i) = \gamma_i + \beta_i p_{i,t}(1 - I_{i,t}) \tag{11}$$

$$logit(e_i) = \delta_i \tag{12}$$

Here, the logit transformation works to constrain both rates between 0 and 1. Colonisation can occur by immigration from outside the transect, γ_i, or by recruitment between patches within the transect, β_i. The latter is hence proportional to current occupancy, and is also subject to competitive and facilitative effects from interactions with neighbours, $I_{i,t}$. The parameter δ_i represents a species' rate of local extinction.

Though interactions between a focal species and its neighbours are often averaged over the whole community (for example Levine and HilleRisLambers, 2009; Godoy and Levine, 2014), they can be both context and species-dependent (Thompson, 1988). To increase biological realism and explore how interactions may vary between groups of species, I elected to average interactions across species belonging to the same guild rather than the whole community. In other words, the effect of one species on another depends not only on the interaction partner's abundance, but also on whether it is a forb (f), graminoid (g), woody species (w) or other (o):

$$I_{i,t} = \alpha_{if} \sum p_{f,t} + \alpha_{ig} \sum p_{g,t} + \alpha_{iw} \sum p_{w,t} + \alpha_{io} \sum p_{o,t} \tag{13}$$

Here, interaction strength α_{i*} is specific to a group of species and their collective abundances ($\sum p_{*,t}$).

Each element of the above Eqs. 11 – 13 can potentially be affected by environmental variation in different ways. Elevation, for example, can affect a species' intrinsic growth rate, fitness, dispersal abilities and seed recruitment. As such, we allowed for a different effect on each of the γ_i, β_i and δ_i parameters when capturing environmental variation (see models 2 to 4 in Table 3). Similarly, interactions between different groups of species could be differentially affected by the same environmental condition. A specific forb's interactions with woody species might not be much affected by elevation, while its interactions with other forbs could be strongly influenced by this factor. To capture this variation between groups in response to abiotic factors, I also applied a different effect for environmental variation to each of the four guilds (model 6 in Table 3). Hence including the effects of both abiotic factors in the model with interactions required the addition of 14 parameters per species.

I evaluated six candidate models operating within the above framework, permuting the inclusion of guild interactions, latitude and elevation. The model with neither interactions nor abiotic factors served as my *null* model. I explored the effect of *latitude* and *elevation* separately and additively (*elevation + latitude*). I also examined a model with interactions but no abiotic factors (*interactions*). Finally, the *full* model included interactions, latitude and elevation. Table 3 provides the names, formulations and number of parameters for each of the evaluated models.

Model name	Model number	$logit(c_i)$	$logit(e_i)$	Number of parameters per focal species
null	1	$\gamma_i + p_{i,t}\beta_i$	δ_i	3
latitude	2	$\gamma_i + g_{iL}L + p_{i,t}\left(\beta_i + b_{iL}L\right)$	$\delta_i + d_{iL}L$	6
elevation	3	$\gamma_i + g_{iE}E + p_{i,t}\left(\beta_i + b_{iE}E\right)$	$\delta_i + d_{iE}E$	6
elevation and latitude	4	$\gamma_i + g_{iL}L + g_{iE}E + p_{i,t}\left(\beta_i + b_{iL}L + b_{iE}E\right)$	$\delta_i + d_{iL}L + d_{iE}E$	9
interactions	5	$\gamma_i + p_{i,t}\beta_i \left\{1 - \left(\alpha_{if}\sum p_{f,t} + \alpha_{ig}\sum p_{g,t} + \alpha_{iw}\sum p_{w,t} + \alpha_{io}\sum p_{o,t}\right)\right\}$	δ_i	7
full	6	$\gamma_i + g_{iL}L + g_{iE}E + p_{i,t}\left(\beta_i + b_{iL}L + b_{iE}E\right)\left\{1 - \left((\alpha_{if} + \alpha_{if,L}L + \alpha_{if,E}E)\sum p_{f,t} + (\alpha_{ig} + \alpha_{ig,L}L + \alpha_{ig,E}E)\sum p_{g,t} + (\alpha_{iw} + \alpha_{iw,L}L + \alpha_{iw,E}E)\sum p_{w,t} + (\alpha_{io} + \alpha_{io,L}L + \alpha_{io,E}E)\sum p_{o,t}\right)\right\}$	$\delta_i + d_{iL}L + d_{iE}E$	21

Table 3: All model formulations and number of parameters.
Measures of elevation (E) and latitude (L) were both scaled. The associated parameters contain $_E$ and $_L$ subscripts, respectively.

Estimating model coefficients

I evaluated the six candidate models separately for each of the 339 focal species in the dataset. Models were implemented in JAGS with R and the R2jags and coda packages (Plummer, 2003; R Development Core Team, 2016; Su and Masanao, 2012; Plummer et al., 2006). Parameters for each species and model variant were estimated independently by using a Markov Chain Monte Carlo algorithm to sample their probability distribution. The algorithm works by constructing several Markov chains which iteratively sample from the expected target distribution of each parameter. All parameters were given uninformative prior distributions. Measures of elevation and latitude were both scaled. Median point estimate values for the γ_i, β_i and δ_i parameters were first estimated from the *null* model variant, and then used as initial values for those parameters in each of the five remaining candidate models.

Initially, I ran each model with three chains and 36 000 iterations. I discarded the intial 31 000 samples and drew samples every five iterations from the remaining 5 000 to construct posterior parameter distributions. I verified each chain for convergence to the target distribution, suitable chain length and autocorrelation between chain steps with the coda package. These tests included the Gelman-Rubin statistic, which verifies whether parallel chains converge to the same target distribution (Cowles and Carlin, 1996), and the Geweke test which checks that the Markov chain is a stationary process and has run the necessary amount of time.

Note that the above tests are indicative only as it cannot be determined with absolute certainty whether a sample taken from a MCMC process is representative of an underlying stationary distribution (Cowles and Carlin, 1996; Dorazio, 2016). Rather, each of the tests can help identify different issues which may arise from running each model. This implies that a given test may indicate nonconvergence even when other tests pass without issue. I therefore permitted final models to fail certain validation tests, as long as a minimum of one test was validated. The above 36 000 iterations were sufficient for 95.8% of total models to reach convergence.

When using a MCMC algorithm, every model should hypothetically be able to reach convergence given a sufficient length of time (Dorazio, 2016). I therefore selected those models which had not yet converged and ran them for an additional 30 000 to 90 000 iterations, once again discarding those samples and drawing the poste-

riors from the final 5 000 interactions. This increased the proportion of converged models to 99.5 % of total models. I chose not to continue running any model which hadn't converged at this stage due to constraints on time and processing power. Models which failed convergence belonged either to the *interactions* or *full* formulations, and were uniformly distributed between guilds ($x^2 = 0.22$), hence I decided it was safe to treat them as missing values.

For those estimates that satisfied the above criteria, I compared the predictive ability of each model using the Deviance Information Criterion (DIC), a Bayesian model equivalent to the Akaike Information Criterion (AIC) (Spiegelhalter et al., 2002). Similar to AIC, DIC is an estimation of model fit based on deviance that includes penalties for increasing the number of parameters; as such, a lower DIC signifies a better fit. As a rule of thumb, a difference in DIC of 3 or more suggests one model predicts the data significantly better than the other (Spiegelhalter et al., 2002). Based on those DIC values, I estimated the best fit model formulation for each of the 339 focal species (models which had not reached convergence were treated as missing values). I calculated ΔDIC as the difference in DIC between each model and the best fit model for that same species. Models with lower ΔDIC values show a better fit to the data.

Analysing model parameters

I investigated the posterior parameter values of the *full* models that had fully converged by this stage, consisting of 330 focal species. Point estimates for each parameter were taken from the median of the posterior distribution. I examined the distribution, mean and dispersion of each parameter across all species, and by species guild. The 'non-woody other' guild was included in the overall analysis and parameter comparison, though I did not make any strong inferences regarding the parameter values for that group given that it only included 11 species.

After verifying the distribution of the δ, γ, β and associated abiotic parameters, I focused the investigation on the parameters determining species interactions. Differences in parameter distributions overall and between guilds were tested for significance with an Anderson-Darling k-sample test, as provided by the kSamples R package (Fritz and Angie, 2016). Parameter dispersion was measured by the quartile deviation, equivalent to half the difference between the first and third quartiles. Joint distributions of parameters were also plotted to explore variance along values of abiotic parameters.

Results

Over all guilds, species richness increased with higher latitude. Species richness did not significantly differ across elevation, though some differences between guilds were visually apparent (Figure 14). In particular, forb diversity tended to decrease with elevation.

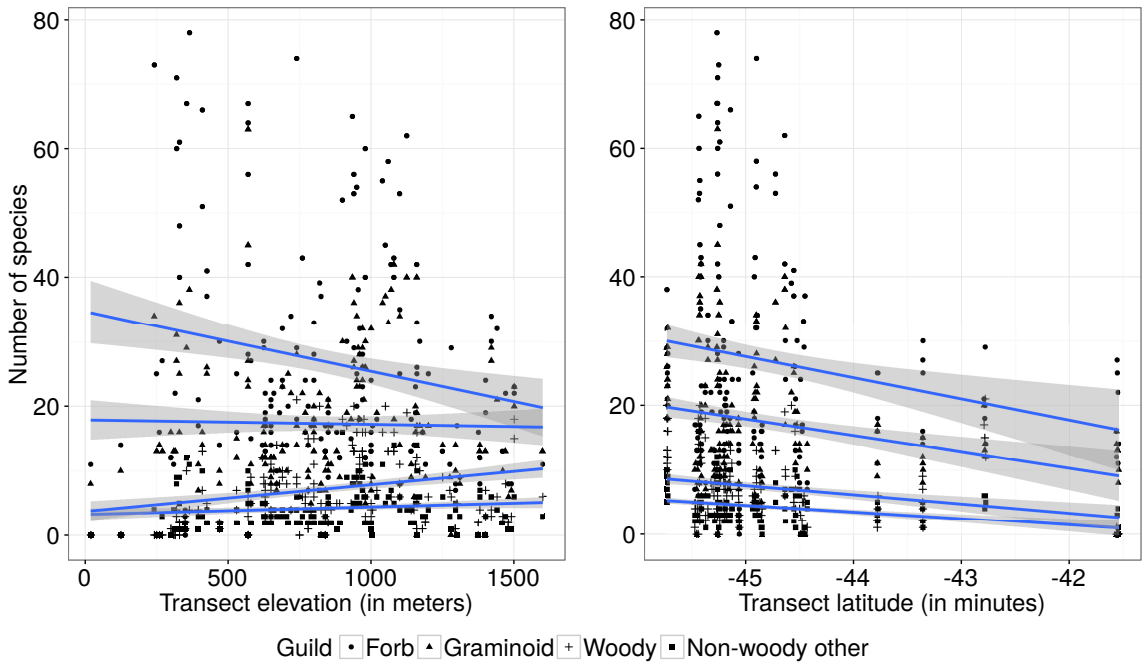

Figure 14: Relationships between species diversity, elevation and latitude, according to focal species guild membership. The lines were fitted using a linear regression, the shaded areas correspond to the 95% confidence intervals.

Evaluating the best predictive model

Overall, the *full* model, which included latitude and elevation and their effect on interactions, provided the best ability to predict changes in abundance for 188 out of 339 focal species (Figure 15). The *interactions* model, which included interactions but no abiotic effecs, ranked next and resulted in a better fit for 83 species. Generally, models which included terms for interactions between guilds performed better than models which didn't. The *null* model and models which included either elevation or latitude without interactions performed similarly to each other, and were almost always worse than the more complex models. There was no significant difference in which model best predicted changes in population abundance among focal species guild ($x^2 = 0.48$)

Though the *full* model usually had the absolute lowest DIC value, it almost always did not differ significantly from the best fit model in

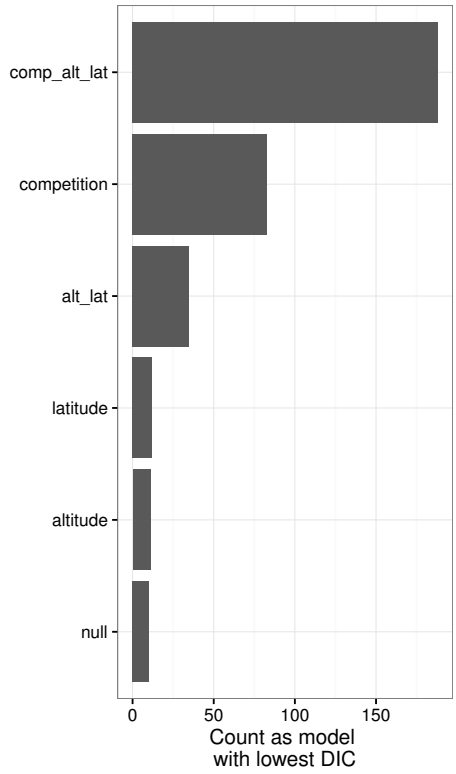

Figure 15: Models sorted by absolute lowest DIC. The x axis refers to the number of species (out of the total 339) for which a certain model formulation has the lowest DIC.

those cases when it did not receive the lowest DIC value (Figure 16); and this was true across all plant guilds. In fact, the *full* model was either equal to or not significantly different from the best predictive model for over 75% of species (Figure 16). These results were robust to the inclusion of models that did not converge. Due to this strong support for the *full* model, I have opted to explore its parameter values across all species for which it reached convergence ($n = 330$) in the rest of the Results.

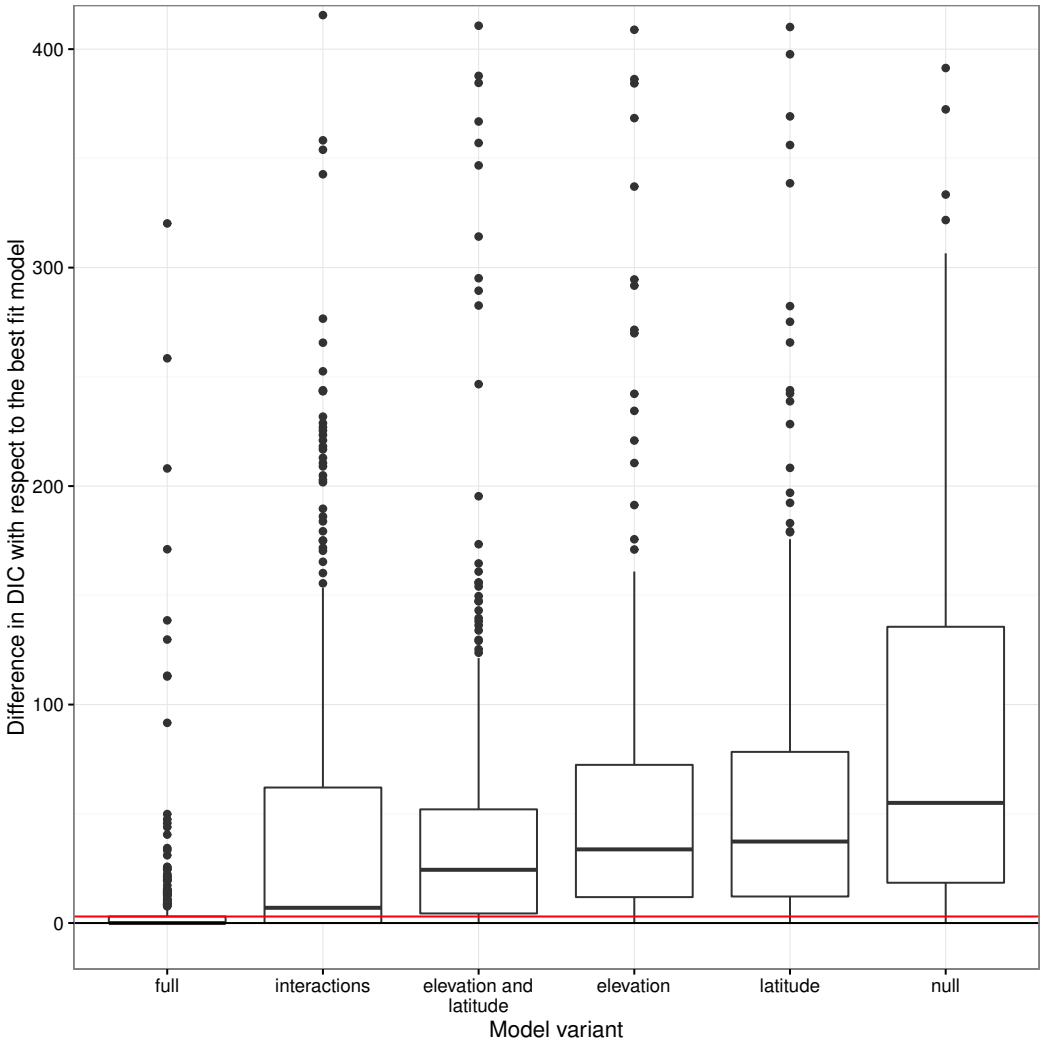

Figure 16: Differences in DIC between the best fit model and each model variant, by species. A ΔDICdifference of 3 or more indicates that one model is significantly better than another, shown by the red line on this figure. All models which fall below the red line are not significantly different to the best fit model for that species. Extreme outlier values were removed across models for clearer presentation.

Interaction parameter	mean	standard deviation	median	quartile deviation
α_{*f}	-0.3053	4.0350	0.0374	1.8158
α_{*g}	-1.7065	4.6778	-0.8080	2.4751
α_{*w}	-0.4326	6.0010	-0.0942	1.9932
α_{*o}	0.3291	5.0982	-0.0259	1.9932

Table 4: Summary table of interaction parameters averaged across all 330 focal species. Due to the model formulation, negative values indicate facilitation whereas positive values indicate competition.

Interactions between guilds

The interactions parameters set to each guild $\alpha_{*g}, \alpha_{*f}, \alpha_{*w}$ and α_{*o} all had significantly different distributions from each other. That is, each guild had significantly different interaction strengths across all focal species. Across all 330 focal species and ignoring abiotic gradients, co-occurring species belonging to the forb (α_{*f}), graminoid (α_{*g}) and woody (α_{*w}) guilds had an average positive effect on focal species immigration between transects (Table 4). The standard deviations for all interaction parameter distributions were large, indicating large variation in the effect of guild interactions between focal species. The α_{*w} parameter showed the largest standard deviation, indicating that the woody species guild had the largest variation in interaction strength with all focal species. Interaction partners belonging to the graminoid guild had the strongest mean positive effect and fewer weak interactions with the focal species than partners belonging to any other guild.

With the exception of interactions with forbs (α_{*f}), the distribution of each interaction parameter was similar across focal species guild, implying that the guild membership of the focal species did not significantly affect interaction strength. In the case of the α_{*f} parameters, their distribution was significantly different a according to guild membership of the focal species. Though interactions with other forbs were on average facilitative, focal species belonging to the graminoid or woody species guild had a mean competitive interaction with forb species. Within-guild interactions were strongly facilitative with the exception of the non-woody other guild, though it si worth recalling that this latter group included species which were very different to each other.

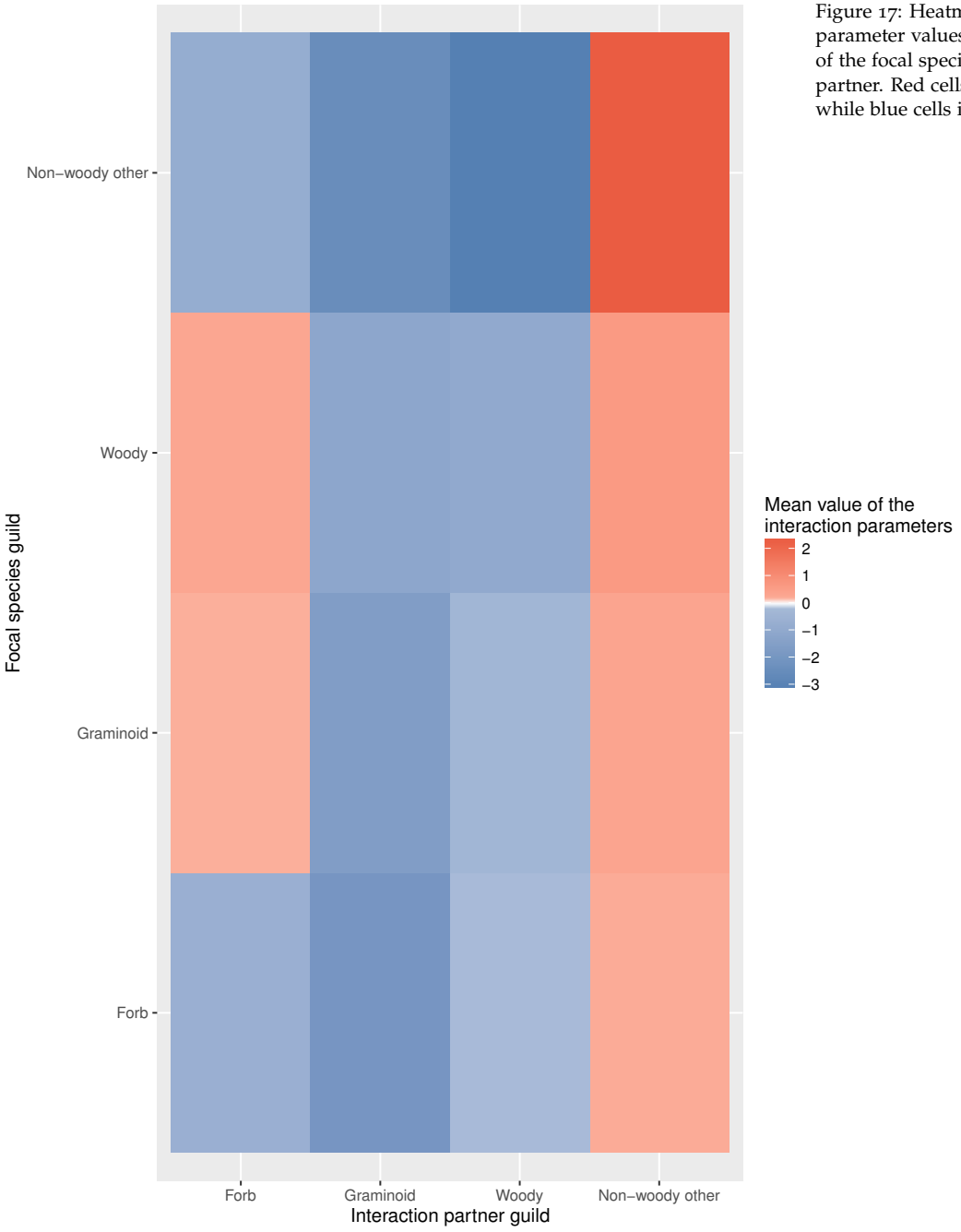

Figure 17: Heatmap of mean interaction parameter values, by guild membership of the focal species and interaction partner. Red cells indicate competition while blue cells indicate facilitation.

	mean effect on extinction rate (δ_*)		mean effect on immigration within transects (β_*)		mean effect on immigration from outside the transect (γ_*)	
	elevation	latitude	elevation	latitude	elevation	latitude
all focal species ($n = 330$)	-1.5541	-1.348	-0.5380	0.4507	-0.4711	2.4680
forbs ($n = 170$)	-0.8993	-0.4304	-0.9753	0.5435	-0.7795	2.5570
graminoids ($n = 86$)	-2.2337	-2.0103	-0.6599	0.6279	-0.4612	2.8805
woody species ($n = 63$)	-2.1601	-3.5297	0.8032	-0.1012	0.2517	1.8604
non-woody others ($n = 11$)	-2.8908	2.1275	-0.5070	0.7925	0.0778	1.3484

Table 5: Mean effects of increasing elevation and latitude on the extinction and immigration rates. Measures of elevation and latitude were both scaled.

Effect of elevation and latitude

Across all focal species, increasing elevation tended to lower the extinction rate (δ_*) and immigration rates (γ_* and β_*). Increasing latitude had a positive effect on both immigration rates and lowered extinction rates, most strongly for woody species (Table 5). Those effects were also seen for focal species belonging to the forb and graminoid guilds. Woody species, on the other hand, showed an average positive effect of elevation on both immigration rates, and a slight positive effect of latitude on immigration from within the transect.

When examining the mean effects of abiotic gradients on each of the interaction parameters, elevation always had a stronger effect than latitude (Table 6). Across all focal species, elevation increased the facilitative effect of interacting forb species on average and increased the competitive effects of all other guilds. The distribution of elevation parameters affecting each of the $\alpha_{*g}, \alpha_{*f}, \alpha_{*w}$ or α_{*o} interaction parameters were significantly different to each other (Anderson-Darling k-sample test, $p < 0.0002$).

Across all focal species, latitude slightly increased the competitive effect of graminoids, forbs and non-woody other species on average, while increasing facilitation with woody species (Table 6). However, the distribution of latitude parameters affecting guild interactions were not significantly different to each other. All abiotic parameters affecting interactions had distributions with large standard deviations, again indicating a wide range of effects over all focal species.

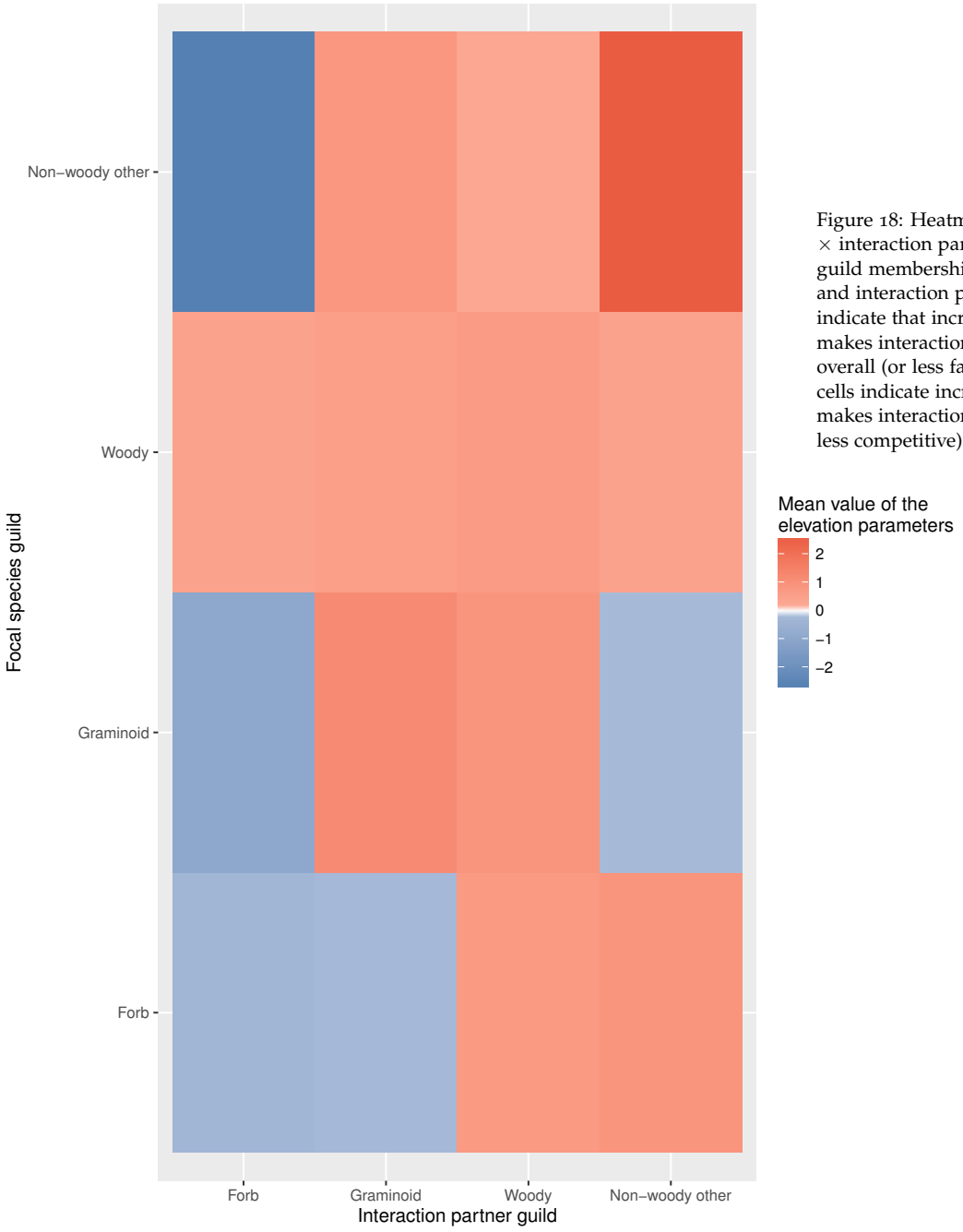

Figure 18: Heatmap of mean elevation $\times$ interaction parameter values, by guild membership of the focal species and interaction partner. Red cells indicate that increases in elevation makes interactions more competitive overall (or less facilitative), while blue cells indicate increasing elevation makes interactions more facilitative (or less competitive).

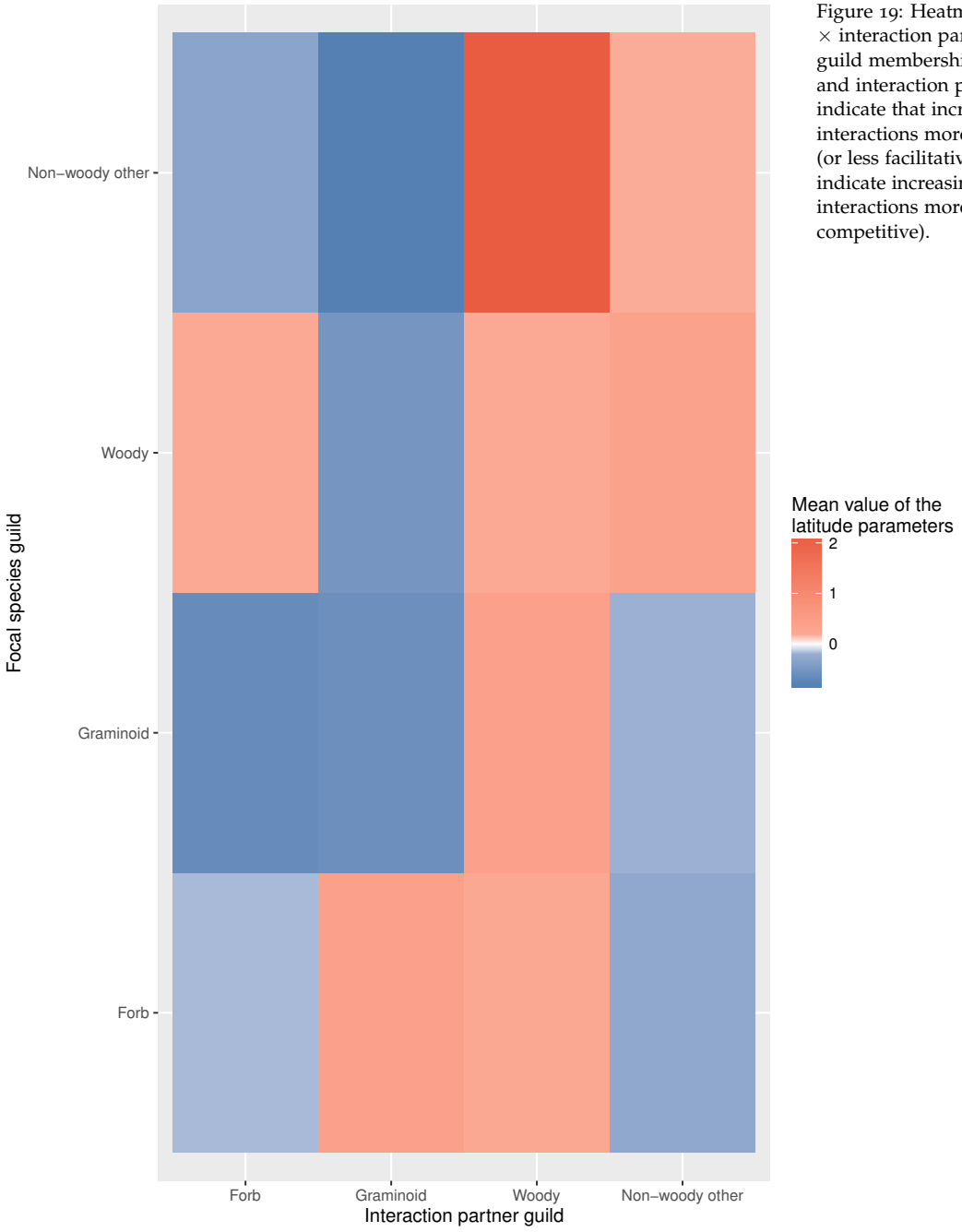

Figure 19: Heatmap of mean latitude × interaction parameter values, by guild membership of the focal species and interaction partner. Red cells indicate that increases in latitude makes interactions more competitive overall (or less facilitative), while blue cells indicate increasing latitude makes interactions more facilitative (or less competitive).

guild membership of the interaction partner	mean interaction strength (α)	mean effect of elevation on α, ($\alpha_{*,E}$)	mean effect of latitude on α, ($\alpha_{*,L}$)
forbs	-0.3053	-0.3969	-0.1677
graminoid	-1.7065	0.3235	-0.0834
woody	-0.4326	0.7078	0.3050
non-woody other	0.3291	0.5690	-0.1106

Table 6: Summary table of interaction parameters across all 330 focal species. Positive interaction strengths indicate competition; negative values indicate facilitation. Positive $\alpha_{*,E}$ and $\alpha_{*,L}$ values indicate that interactions become more competitive (or less facilitative) as elevation or latitude increases.

Contrary to expectations, the effects of elevation and latitude on the guild interaction strengths were not significantly different according to guild membership of the focal species. Nevertheless some of the differences in mean values are worth noting (Figure 18 and 19). Increasing elevation and latitude tended to increase the facilitation (or lower competition) of forb species on all others, except when forbs were interacting with woody species. On average, the interactions of graminoid species tended to become less facilitative with elevation and more facilitative with latitude. However the the effect was reversed when the focal species was a forb, such that the effect of graminoids on forbs became more facilitative with elevation and less so with latitude. Finally, elevation tended to make within-guild interactions less facilitative, except for forbs interacting with other forbs (Figure 18).

Discussion

Within this study, I compared a series of nested models based on how well they each predicted changes in plant abundance. The *full* model, which included interactions between guilds that varied with elevation and latitude, performed best overall. Models with interactions almost always performed better than models that only included the effects of elevation and latitude, which suggests that interactions between species were a stronger driver of population dynamics than elevation or latitude. I therefore recommend that future models predicting changes in New Zealand grassland plant abundances consider including the effects of plant-plant interactions in their models, a result that is also in accordance with the results from the previous chapter.

Of all candidates explored, the best model included different interaction strengths for each guild that also varied across abiotic gradients. Overall, different focal species interacted differently with species from each of the four guilds (forbs, graminoids, woody species and non-woody others). Elevation and latitude had variable effects on these interactions, with increases in both associated with

weaker interactions with some guilds and stronger interactions with others. Of note, these collective observations point to complex relationships between species interactions and abiotic factors which are likely not captured by linear models, such as those predicted based on the general stress-gradient hypothesis (SGH).

Interactions between focal species and guilds

Overall, the effect of interactions depended more strongly on who the focal species interacted with rather than which group the focal species belonged to. It would be worthwhile to compare these results to other interaction types such as plant-pollinator mutualisims or non-trophic interactions in food-webs. The results of this study could also help simplify future studies exploring the context-dependency of interactions by suggesting that variation in interactions could be better explained by characteristics of the interaction partner rather than the focal species (Moen and Meurk, 2001; Peltzer and Köchy, 2001).

The interaction strengths between focal species and functional guilds were also uncorrelated when compared across focal species, indicating that the effect of interacting with one guild did not help inform about the effects of interacting with any other guild. As such, this may lead to incorrect generalisations when assessing interaction strength across diverse neighbourhoods. For example, interactions between a forb species and members of the graminoid guild might be strongly facilitative, while interactions between that same forb and woody species were weakly competitive. This indicates that the competitive hierarchies within New Zealand grasslands are highly variable depending on the focal species, and perhaps better investigated by examining competition under the lens of trade-offs between competitive effect and competitive response (Grace and Tilman, 1990; Moen and Meurk, 2001). These differences in interaction strength between guilds would not have been apparent if averaged across the whole community, and underlines the importance of making careful decisions when simplifying and summarising relationships within a community (Levine and HilleRisLambers, 2009; Godoy and Levine, 2014).

Though the growth forms by which plants were grouped in this study reflected overall similarities in functional traits (Diaz et al., 1997), it is clear that these groups were quite broad and in the case of the 'other' group contained functionally very different types of species. Thus, there was undoubtedly a lot of within-group variation

in stress-tolerance and resource use within guilds assessed in this study (Wardle, 1991). In all likelihood, this limitation of my dataset played at least some part in the large standard deviations observed for each distribution of guild interactions. A more fine-grained approach that averaged effects across the community based on more specific traits such as above-ground biomass or rooting depth, would likely uncover even stronger relationships than those identified here (Tilman, 1990). Perhaps not surprisingly, that approach has recently been championed for predicting interactions within other systems, especially amongst plant-pollinator communities (Schleuning et al., 2015; Coux et al., 2016).

Variation in interaction strengths along abiotic gradients

Both elevation and latitude had different effects on interactions between focal species and each of the four guilds. First, the effects of elevation and latitude on interactions varied in magnitude, and were at times oppposite, highlighting the need to investigate variation in interaction effects across multiple abiotic stressors. Second, both abiotic gradients had a different effects on interactions depending on the guild of the interaction partner.

Within the New Zealand communities represented here, increasing elevation is typicallly associated with lower mean temperatures, lower soil moisture and nutrient content, and higher wind stress (Cossens, 1987; Chapman and Bannister, 1990). Plants at higher latitudes also experience colder temperatures, as well as weaker light intensity and more variable photoperiods throughout the year. Both gradients therefore equate to more stressful environments, albeit in slightly different ways. According to the traditional SGH, interactions should be observed to become less competitive or more facilitative along both these gradients (Bertness and Callaway, 1994; Callaway, 1995).

Precisely as suggested by the SGH, interactions between focal species and members of the forb guild became, on average, more facilitative with increasing elevation and latitude. Interactions with the graminoid and woody species guild also became weaker upon moving higher up both gradients, but in the opposite direction to that predicted by the SGH: less facilitative, and in the case of woody species, even slightly competitive at higher elevation. In their revision of the SGH, Maestre et al. (2009) proposed that variation in the general SGH pattern is in part due to trade-offs between stress-tolerance and competitive ability of the interacting partners. Within this con-

text, forb species are likely to be the least adapted to cold temperatures or low humidity compared to members of the graminoid and woody guild. They typically die back during the winter, and when found at higher elevation they are often seen growing alongside or between tussock grasses, hypothetically for protection from the wind (Wardle, 1991).

On the other hand, both woody and graminoid guilds contained many alpine species which are well-adapted to conditions associated with higher elevation and latitude. Though some graminoid species do die back in the winter, many species in this study were native tussock-forming grasses which do not completely die back (e.g. members of the *Chionochloa, Festuca,* and *Poa* genera, and some members of *Carex* and *Rytidosperma*, Cockayne, 1910). The clumped growth form of tussock grasses makes them more tolerant to wind stress, and they typically have long roots which can reach moisture more deeply than other grasses (Cockayne, 1910), an advantage in lower-humidity alpine grasslands. In contrast to forbs and graminoids, elevation increased colonisation rates for the woody species guild. Native shrubs and sub-shrubs such as members of *Raoulia* or *Celmisia* genera are likely to have freeze-tolerance mechanisms, dense growth forms to tolerate wind and small leaves to minimise water loss (Allan, 1982). These attributes would confer them an advantage over both graminoids and forbs under more stressful conditions, and could reasonably lead to increases in their competitive ability as observed here.

Though the SGH concept has received wide support (Callaway, 2007), other studies have found that variation in the intensity and overall outcomes of interactions along stress gradients is highly dependent on the nature of the stress gradient involved (Kawai and Tokeshi, 2007) and the characteristics of the focal species (Choler et al., 2001). Given that New Zealand alpine grasslands are typically dominated by graminoids and woody species, and members of those guilds are well-adapted to the conditions associated with higher elevation and latitude (Moore, 1955; Mark et al., 2013), the switch from higher to lower facilitation along the two gradients could simply reflect that the optimum abiotic conditions for these two groups is at higher elevation and latitude. In the case of woody species, this is supported by the fact that elevation also had a positive effect on the colonisation of new patches regardless of the effect of interactions. Maestre et al. (2009) suggested that variation in the general SGH pattern could be explained by whether the stress gradient was driven by resource limitation, and by trade-offs in stress-tolerance

versus competitive ability between plants. Results from this current study suggest that stress-tolerance and competitive ability are intimately linked, and this dataset and model framework could provide a good starting point for testing the specific hypotheses laid out by Maestre et al. (2009). For example, they predict that the effect of a species with traits promoting relative competitive ability under high resource-limited stress (e.g. low water or nutrient availability) will be facilitative when interacting with a stress-tolerant species but competitive when interacting with another competitive species.

Study limitations

When fitting my models, I simplified interactions between species so that interaction strength only varied according to the guild of the interaction partner. The rationale was that this simplification was more biologically realistic than ignoring interactions or generalising over the whole community, and avoided the computational demands associated with modeling every species pairwise interaction (see the previous chapter). Whilst I attempted the latter, I also abandoned it once it became clear that models with such a high number of potential pairwise interactions ($n = 339$) would take too much time and computational effort to converge. The processing speed of such models can of course be improved upon, and perhaps another such attempt should be made in the future, but it was outside the scope of this present study. Nevertheless, species guilds such as forbs, graminoids and woody species correspond to clear differences in growth form and general life-history strategies (Walker, 2000), and are hence useful groupings by which to explore interactions in natural communities (Diaz et al., 1997; Díaz et al., 2016). This is exemplified here by the fact that the overall distributions of interaction strengths between each interaction partner guild were significantly different to each other.

I also note that this study has only allowed elevation and latitude to have linear relationships with interaction strengths and the extinction and colonisation rates. This necessarily meant that hump-shaped relationships, which occur when a species' optima is somewhat in the middle of its experienced range of environmental factors, and other nonlinearities could not be captured. Fitting models which allow for non-linear relationships between interactions and environments should improve on this issue, though they are also susceptible to the computational issues highlighted above.

In addtion, I elected to restrict my exploration of abiotic effects on interactions to elevation and latitude given data availability. While both serve as suitable proxies for several environmental stress gradients (temperature, soil humidity and wind stress for example), the plant communities present in this study respond to a wider range of abiotic conditions than those captured purely by elevation and latitude. Not only that but levels of stress severity can vary over time and space. Events such as extreme temperatures, periods of drought or heavy rainfall can alter the competitive hierarchies and have effects on patterns of coexistence (White et al., 2001; Everard et al., 2010). Herbivory, though biotic, has also been shown to have significant effects on community competition in New Zealand grasslands and alter competitive dominance between species (Lord, 1974; Wraight, 1964) but was not included in the model. As such, including a wider range of stress gradients (e.g. precipitation) or more precise measures of stress (e.g. temperature) could improve further predictions and potentially weaken the relative importance of interactions on population dynamics in this framework.

Conclusion

The relationships between plant-plant interactions and how they are affected by abiotic factors are complex and variable, but including them in models of plant population dynamics clearly improved our ability to predict changes in plant abundances. Averaging interaction strengths across functional guilds provided an easy and tractable way of generalising interaction effects while keeping the amounts of data and computing time within the limits of feasability. Increasing elevation and latitude made interactions with some guilds weaker and those with other guilds stronger, which highlights how extensively the outcomes and effects of interactions vary across a landscape depending on the biotic context (Mod et al., 2016). In the case of New Zealand grasslands, the results from this study suggest plant stress tolerance is strongly linked to interaction outcomes under varying environmental conditions. Furthermore, grouping species according to functional traits related to stress-tolerance might be advantageous where such information is available and would likely help uncover more strongly supported relationships between groups of interaction species (Kunstler et al., 2016).

Synthesis

In this thesis, I have investigated how interactions between species can improve our predictions of population dynamics in natural grassland communities. First, I explored how interactions could be included, and whether incorporating every pairwise interaction was feasible and an improvement over averaging interaction effects across the community. Second, I considered how two specific abiotic gradients might affect interactions between guilds of species. Taken together, the results of these studies have clear implications for the study of species interactions and the improvement of population dynamics models. Furthermore, they help uncover which species strongly interact, and how the outcome varies under different conditions — factors crucial in predicting how grassland communities will respond to disturbances and climate change.

Species interactions

In *"Quantifying the impact of interactions in New Zealand grassland communities"*, I found that including the effect of every pairwise interaction improved model predictions of population dynamics, despite the high parameterisation and model complexity. Though models quantifying all interaction strengths across a community have been suggested by several previous studies (Adler et al., 2007; Levine and HilleRisLambers, 2009; Godoy and Levine, 2014; Kraft et al., 2015), they have very rarely been attempted due to the amount of data and processing required. Admittedly, averaging the effects of interactions across the whole community did improve performance compared to ignoring interactions altogether, but was far from providing the improvement of the full model.

The distribution of interaction strengths was dominated by many weak interactions and few strong ones, as suggested by theoretical studies (Kokkoris et al., 2002; Fowler, 2010, 2013) and measures of interaction strength in other types of communities such as food webs (Paine, 1992; Neutel et al., 2002). This pattern allows for greater

system stability by limiting knock-on effects and the spread of disturbances throughout the community (McCann et al., 1998). Within this context, I therefore show that plant communities show similar interaction patterns to those found in predator-prey systems, and that NZ grasslands appeared to be relatively stable communities.

In this study, neither competitive nor facilitative interactions strongly dominated either community, suggesting both types of interactions are important to New Zealand grassland communities, as in other plant and grassland systems (Bertness and Callaway, 1994; Callaway and Lawrence, 1997; Holmgren et al., 1997; Wright et al., 2013). I also found that groups of exotic species interacting with exotics had more strong interactions than groups of native species interacting with natives. Past research has suggested invasive species might generally be stronger competitors than natives, for reasons such as the evolution of novel adaptations and release from coevolved herbivores (Callaway and Ridenour, 2004; Vila and Weiner, 2004; Riley et al., 2008; Porté et al., 2011; Parker et al., 2013; Zheng et al., 2015). My results are therefore in line with this growing body of research.

In *"How plant interactions vary by guild and along two abiotic gradients"*, I suggest that biotic interactions were a stronger driver of population dynamics in this system than elevation or latitude. I found that interactions between focal species and each of the four defined guilds were significantly different, as suggested by other studies linking functional traits to competitive ability (Kunstler et al., 2016). In particular, graminoid species tended to have strong facilitative effects at low and mean elevations when compared to other guilds.

However, guild membership of the focal species was surprisingly uninformative about interaction strengths. As estimating every species pairwise interaction strength was not feasible, averaging interactions across guilds was an intuitively appealing way of simplifying biotic interactions (Diaz et al., 1997). Though it contrasts with the results from the previous chapter, it was critical in allowing me to link general guild traits to variation in interaction outcomes along abiotic gradients. Futhermore, the absence of a strong pattern between focal species guild underlines how variable the competitive hierarchies occurring in New Zealand grasslands can be.

Environmental effects on species interactions

In *"Quantifying the impact of interactions in New Zealand grassland communities"*, I argued that variation in the overall distribution of in-

teraction strengths could be related to the elevation of different sites. In particular, the community from the highest elevation site showed a more restricted distribution of interaction strengths and a higher density of weak interactions. Within this context, community stability had a positive relationship with increasing elevation, suggesting that alpine grassland communities might be more resilient to disturbances (De Ruiter et al., 1995) and extinction (Fowler, 2013) than low or mid-elevation grasslands.

In order to clarify the potential interacting effects of community composition and environmental conditions on interaction strengths, in *"How plant interactions vary by guild and along two abiotic gradients"* I hence asked whether interactions with different guilds were differentially affected by environmental gradients as hypothesised by Mod et al. (2016). I found that the effects of elevation and latitude varied according to which guild a focal species interacted with. As sites increased in elevation and latitude, interactions with forbs species became more facilitative. However, interactions with graminoids and woody species — which are generally considered to be better adapted to these stressful conditions — became less facilitative if not outright competitive. In this system, variation in interaction effects along those abiotic gradients hence seems to be linked to both competitive ability and stress tolerance (Maestre et al., 2009).

Implications for theory and applications

This thesis has several implications for ecological research. The development of a new model framework tailored to the publicly available data used in both studies can, for example, be applied to further research conducted on this same or similar datasets. Additionally, the results highlighted the importance of species interactions in plant communities and how they might be affected by abiotic gradients, which sheds lights new insights into dynamics of New Zealand grassland communities and can inform future models of plant population dynamics.

Devising the final model framework used throughout this thesis was a challenging task, with my original formulation going through several iterations before converging on the Levins (1970) and Theory of Island Biogeography (Mac Arthur and Wilson, 1967) hybrid upon which all subsequent models were based. Developping these ensuing models also required diligence and a meticulous approach. The versatility of this framework makes it appropriate for further exploration of the factors affecting plant population dynamics in this system,

for example simplifying interaction effects by functional traits, or incorporating other abiotic gradients.

Both studies presented here highlight the need to include interactions with neighbours when attempting to improve predictions of plant population dynamics. Estimating every pairwise interaction strength is a complex and intensive task, but using large, long-term datasets and appropriate statistical methods can help us circumvent some of these difficulties (Ives et al., 2003; Pantel et al., 2014). Simplifying interactions, for example by averaging effects across guilds as in *"How plant interactions vary by guild and along two abiotic gradients"*, can also provide a good compromise between estimating every pairwise strength and oversimplifying interactions, especially in situations where the former is too computationally demanding. Though this midway approach does not provide an explanation for how interactions between plants can be summarised, it does provide greater predictive power than averaging interaction across the whole community (see Shmueli, 2010, for a disambiguation of explanatory vs. predictive modeling).

"How plant interactions vary by guild and along two abiotic gradients" also highlighted two additional factors to consider when exploring the effects of interactions on population dynamics. First, different environmental gradients can have different effects on interactions, but often covary and a rarely independent, hence the need to study interactions under multiple abiotic gradients at the same time. Second, interactions with different groups of species can also differ in their response to those gradients. This variability in gradients, interactions, and their relationship to each other is especially vital when aiming to predict how species abundances and dynamics might vary with climate change, given that not all plants or interactions will respond similarily (Alexander et al., 2016).

From a more applied perspective, both studies suggested several factors contributed to the stability of grassland communities. Community stability increased with higher elevation, and with a higher proportion of native to exotic species, in agreement with other studies of New Zealand grasslands (Meurk et al., 2002). Whether the latter is a reflection of differences in the competitive ability of exotic species (Callaway and Ridenour, 2004; Porté et al., 2011), or of the functional guilds which they disproportionately belonged to (forbs and graminoids), was unclear. Irregardless, it is likely that the destabilisation of grassland communities associated with exotic species is caused by as small subset of strongly interacting invaders (Gross

et al., 2015; Zheng et al., 2015), which also experience a weakening of interactions with elevation.

"How plant interactions vary by guild and along two abiotic gradients" and other studies (Walker, 2000; Moen and Meurk, 2001) have highlighted the variability of competitive hierarchies in New Zealand grassland communities. Differences in how interactions with each guild varied along abiotic gradients further complicates our ability to generalise the outcomes of interactions across these grasslands. Nevertheless, graminoid species tended to have a strong facilitative effect on focal species at lower elevations, whereas forbs tended to have a strong facilitative effect at higher elevations. By virtue of these strong interactions, species belonging to these groups might hence have disproportionate effects on the abundances of other plants in the community (Soulé et al., 2005). Identifying such 'keystone species' in the context of plant communities (Gordon, 1998; Nyakatya and McGeoch, 2008) has several applications for the management of grasslands, such as their potential use as indicator species or identifying where to focus conservation effort. These results also highlight that grasslands occurring under different conditions — lowland, mid-elevation and alpine — are more sensitive to variation in different groups of species; these communities are hence most susceptible to different threats and must be managed accordingly (Walker et al., 2003; Mark et al., 2013).

The estimates for pairwise interaction strengths from *"Quantifying the impact of interactions in New Zealand grassland communities"* required access to a large, replicated dataset. Additionally, results from *"How plant interactions vary by guild and along two abiotic gradients"* would not have been as impactful had the data not been sampled across such a range of elevational and latitudinal gradients. Elevation tended to lower colonisation and extinction rates, dampening oscillations in plant abundance and frequency (Grime, 1977) which means the full effects of interactions might not have been captured within the sampled timeframe (Coomes and Allen, 2007). This underscores the importance of long-term vegetation monitoring at broad spatial scales for uncovering patterns and drivers of grassland community composition (Meurk et al., 2002; Day and Buckley, 2013; Young et al., 2016), especially for communities occurring at higher elevations..

Future directions

The methodology used in this thesis can be improved upon in several ways. I used available R packages (rjags and R2jags, Plummer,

2003; Su and Masanao, 2012) to implement the MCMC algorithms and posterior analysis used in both studies. However, writing algorithms 'from scratch' specific to the model framework could significantly speed up convergence times and further uptake. Other MCMC techniques such as simulated annealing could also help converge the multi-modal posterior distributions and provide more reliable or precise estimates of interaction strengths (Kirkpatrick et al., 1983; Geman and Geman, 1984). Finally, many methods of Bayesian model selection exist though there is no general consensus on which is best, and it would be valuable and interesting to see how sensitive the results are to which measure of goodness of fit is used. I chose DIC because of its similarity to AIC; it is also less computationally expensive than out-of-sample methods and is already calculated as part of the R2jags package. However, it can be less reliable when there are multiple modes to the posterior and be sensitive to parameterisation (Hooten and Hobbs, 2015; Broms et al., 2016). I hence suggest future analyses attempt model selection by cross-validation (which can be even more computationally demanding) or posterior predictive loss, which is appropriate for multi-modal posteriors and time-series data (Hooten and Hobbs, 2015).

One of the advantages of using a Bayesian framework is the ability to incorporate prior knowledge into models. This means that the models used in both studies here can be complemented by constraining the priors. For example, if an interaction between two species is known to be competitive, the corresponding interaction strength can be given a positive or negative prior distribution as appropriate. This information can come from knowledge of natural history, other tested models or experimental results. Because of this, verifying the predictions made here with experiments or mechanistic models can in turn improve later model predictions. Additionally, the reverse is also true. Results from the studies presented here can be incorporated as priors into subsequent models. For example, interactions which were found to be very weak would be assigned very low prior values, effectively informing the interaction strengths of future multi-species models (Wootton and Emmerson, 2005).

In *"Quantifying the impact of interactions in New Zealand grassland communities"*, I produced estimates of pairwise interactions in that community. These estimates can be used to investigate a variety of questions centered around the role and patterns of species interactions in plant communities. For example, in order to compare the importance of niche and neutral mechanisms in driving coexistence, Adler et al. (2007) suggest fitting intra and interspecific interaction

coefficients, and per capita growth rates in the absence of density effects, to a time-series of plant abundances. The fitted parameters can then be used to quantify fitness equality and stabilising mechanisms, which directly relate to niche and neutral processes. Alternatively, estimating pairwise interaction strengths also identifies important interaction partners. By ignoring non-significant interactions and drawing the focus to strong interactions, plant communities can also be represented as networks of interacting plants, similarily to how food webs are often depicted (Elton, 1927; May, 1973; Pascual and Dunne, 2006). This would then allow the application of graph theory to the analysis and comparison of plant community networks (Strogatz, 2001; Dunne et al., 2002; Pavlopoulos et al., 2011).

In *"How plant interactions vary by guild and along two abiotic gradients"*, I chose to simplify interactions by averaging effects across species guilds. A more fine-grained approach, averaging effects according to more specific traits, could uncover stronger relationships. Such approaches have already been successfully applied to woody species, uncovering strong relationships between functional traits and interaction strengths (Kunstler et al., 2012, 2016; Fortunel et al., 2016). Considering the link revealed by this present between variation in interaction outcomes and stress-tolerance, I would recommend the use of functional traits linked to stress-tolerance or competitive ability in grasses. Maestre et al. (2009) suggested that trade-offs between the two might drive deviations from the typical stress-gradient pattern, which provides a clear set of hypotheses to test and explore patterns of variation in interaction strength.

Both studies presented here, and others (for example, Moen and Meurk, 2001; Walker et al., 2003; Rose and Frampton, 2007) point to the existence of complex relationships between competitive effects, exotic species and their traits in New Zealand grasslands. Grasses exotic to New Zealand have been shown to significantly differ from natives in their functional traits, but only a small subset tend to strongly outcompete natives (Gross et al., 2015). I suggest that combining both approaches presented in this thesis — measuring the effects of pairwise interaction strengths as in *"Quantifying the impact of interactions in New Zealand grassland communities"* and linking those to functional roles or traits as in *"How plant interactions vary by guild and along two abiotic gradients"* — can help us identify which exotic species are likely to significantly affect grassland communities and hence better focus management efforts. This is especially important given that these communities will have to face new competitors under climate change (Alexander et al., 2016).

Conclusion

While there is a wealth of research on the effects of plant-plant interactions, the mechanisms which mediate them, and their context-dependency, there are still many surprising gaps in our knowledge. Here, I have found that these interactions are strong drivers of plant population dynamics at broad spatial scales and in diverse, natural communities. The relationship between the identity and traits of interaction partners, and their adaptation to environmental conditions, determines the outcome and intensity of plant interactions. The research presented here provides a robust framework for investigating interactions in natural plant communities, improving our predictions of plant population dynamics, and sheds light on some of the processes promoting variation in interaction strength. Exploring how plant interactions can be affected by the relationships between abiotic gradients, exotic or native species status and functional guild can help us identify how the grasslands studied here will vary ion their response to future threats.

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Acknowledgments

First and foremost, I would like to thank my primary supervisor, Daniel Stouffer, who provided me with guidance, support and mentorship throughout this thesis, and continually encouraged me to improve. His supervisorship has been crucial in my scientific development and my enjoyment of the challenges of academia. I would also like to thank my secondary supervisor, Margie Mayfield, for providing me with continued support and encouragement, as well as new perspectives and opportunities.

A big thank you to Alyssa Cirtwill, Matthias Dehling, and Carla Gomez Creutzberg for comments on manuscripts. I would also like to thank all my lab mates for their advice, their help and their words of encouragement: Alyssa Cirtwill, Bernat Bramon, Camille Coux, Carla Gomez Creutzberg, Giulio Dalla Riva, Fernando Cagua, Marilia Gaiarsa, Matthew Hutchinson, and Matthias Dehling. From coding to writing, you all took the time to answer my questions and help whenever I needed it.

Thank you to the National Vegetation Survey databank and all whom contributed data and permitted me to use it for this project. In particular, thank you to Elise Arnst for handling all my requests and fielding my technical questions. I would also like to thank the biology computer cluster and its administrator, Steve Gourdie — this thesis would not have been possible otherwise.

I am grateful to my sources of funding, the Miss E. L. Hellaby Indigenous Grasslands Trust and the University of Canterbury Masters Scholarship. I also like to acknowledge the Royal Society of New Zealand Canterbury Branch Travel Award, the Graduate Women Canterbury Trust Travel Award and the School of Biological Sciences Travel Grant, all of which suported my travel to the *"Unifying Ecology across Scales"* Gordon Research Conference and Seminar 2016.

Last but not least, thank you to Montgomery and my family for their endless support, love and encouragement.